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INTENSIVE FOREST HARVEST :

A REVIEW OF NUTRIENT BUDGET CONSIDERATIONS

by

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ABSTRACT

It is clear that the use of intensive harvest techniques, such as whole-tree or complete-tree clear-cutting, will produce substantially higher yields of biomass than would conventional bole-only clear-cutting of the same stand. However, these increases in biomass yield are accompanied by much larger increases in the removal of nutrients, due to the removal of nutrient-rich tissues in the intensive harvests. Thus, the short-term biomass gains are purchased at the longer-term expense of accelerated nutrient removals. These nutrient removals can be further increased by severe disturbance of the site during logging or subsequent site preparation.

Simple calculations indicate that, for short-rotation Populus plantations, the nutrient removals with whole-tree-harvested biomass would result in a relatively rapid nutrient impoverishment of the site. On the other hand, medium or longer-term rotations result in more moderate calculated removals of nutrients with harvested biomass, which appear to be of less ecological significance. However, due to variations and other uncertainties in many of the data upon which these calculations were based, these conclusions are tentative. Longer-term studies are required, including further refining and field-testing of forest growth models.

RESUME

Il est évident que l'emploi de techniques de récolte intensive, telles que la coupe rase par arbres entiers ou au complet, produira des rendements en biomasse substantiellement plus élevés que la méthode classique de coupe rase des fûts seulement du même peuplement. Toutefois, ces accroissements de rendement en biomasse s'accompagnent d'accroissements de prélèvement d'éléments nutritifs de beaucoup plus élévés, du fait que des tissus riches en ces mêmes éléments sont prélevés par les récoltes intensives. Ainsi donc, les gains à court terme en biomasse se soldent à long terme par des prélèvements accélérés d'éléments nutritifs, qui peuvent être encoure accentués par la grave perturbation résultant des opérations d'exploitation ou de préparation subséquente de la station.

Des calculs simples montrent que, pour les plantations de Populus à courte rotation, le prélèvement d'éléments nutritifs qui s'opère avec la récolte de biomasse par arbres entiers aboutirait à un appauvrissement relativement rapide de la station. Par contre, des rotations à moyen ou à long terme se traduiraient par des prélèvements calculés plus modérés avec la biomasse récoltéé, ce qui semble avoir un impact moindre sur l'écologie. Toutefois, en raison des variations et autres incertitudes afférentes à beaucoup des données sur lesquelles ces calculs ont été étayés, les conclusions ci-dessus sont hypothétiques. Des études de plus longue haleine s' imposent, y compris le perfectionnement et l'expérimentation in situ de modèles de croissance forestière.

FOREWORD

ENFOR is the bilingual acronym for the Canadian Forestry Service's ENergy from FORest (ENergie de La FORêt) program of research and development aimed at securing the knowledge and technical competence to facilitate in the medium to long term a greatly increased contribution from forest biomass to our nation's primary energy production. This program is part of a much larger federal government initiative to promote the development and use of renewable energy as a means of reducing our dependence on petroleum and other non-renewable energy sources.

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1. INTRODUCTION

Forest-related industries collectively comprise one of Canada's largest industrial sectors. Total outputs in 1978 were some $18 billion, and the sector, directly accounted for some 300,000 jobs (Anon. 1978). At present, the forest industries mainly utilize trees as sources of structural materials or fibre. However, with the rising costs and dwindling reserves of energy derived from non-renewable hydrocarbon resources, attention is also focusing on the potential for the use of forest biomass as a renewable source of energy. In a country such as Canada, having ca. 37% of its land area forested [3.4 x $10^6 km^2$, ca. 10% of the productive forest lands in the world (Bowen 1978)], tree biomass has the potential to displace significant quantities of fossil fuel energy (e.g., Evans 1974; Anon. 1976 a,b,; Love and Overend 1978; Jones et al. 1979; Henry 1980).

To maximize the short-term economic returns from forest management and harvest for materials or energy purposes, it is likely that intensive removals of biomass will occur over increasingly larger tracts of forest. For example, whole-tree (above-ground), and possibly even complete-tree (above and below-ground) harvesting may be used extensively. Although these harvest methods greatly increase the biomass yields per unit of forest land, they generally increase nutrient removals by substantially larger factors. At present, the ecological consequences of these accelerated rates of nutrient removal from forest stands are not understood, largely due to a paucity of site, species, and element-specific data relevant to: i) nutrient removals during forestry operations, ii) the sizes of the nutrient pools in total and plant exploitable forms in various residual soil compartments, iii) the net accretions or depletions of the various nutrients in both cut and uncut stands, and iv) the degree of nutrient limitation of forest productivity. In addition, even where these data are available, we have an incomplete understanding of how these and other factors interact ecologically to determine site productivity.

Because of the greatly-accelerated rates of nutrient removals in whole-tree or complete-tree harvested forests (frequently exceeding nutrient removals by conventional clear-cutting by factors of 2-3), it seems reasonable to envisage future deterioration of many sites. Further evidence for this is found in the observation that the productivities of most forest stands in Canada are to some degree nutrient-limited, especially with respect to the rate of supply of nitrogen in an assimilable form (e.g., Hegyi 1974; Armson et al. 1975; Weetman et al. 1974, 1976; Czapowskyj 1977; Ballard 1979; Tamm 1979). We might further envisage that site deterioration via nutrient impoverishment would be especially severe on the more intensively-cropped sites (i.e., sites where whole-tree or complete-tree clear-cuts are used over short rotations), or perhaps on sites that are initially sensitive to nutrient impoverishment following cutting (perhaps because of initially low quantities in the soil nutrient pools, or susceptibility to soil erosion following cutting), unless steps are taken to subsequently ameliorate decreased site fertility, for instance by forest fertilization.

It is notable that several authors and two recent symposia have expressed a real concern over the possible deterioration of forested sites due to accelerated nutrient depletions via intensive biomass removals (e.g., Rennie 1955; Keeves 1966; Tamm 1969;

Boyle and Ek 1972; Weetman and Webber 1972; Kimmins 1974, 1977, 1980; White 1974; Calef 1976; Norton and Young 1976; Anon. 1977, 1979; Glesinger 1977; Hornbeck 1977; Aber et al. 1978, 1979; Wells and Jorgensen 1979; White and Harvey, 1979; Carlisle 1980; Kimmins et al. 1980). Significantly, complete agreement does not exist among these various authors as to the ecological significance of the removal of large quantities of particular nutrients with harvested biomass. This overall lack of consensus is due to a number of factors, especially: i) species and stand-age differences in nutrient removals from harvested sites, and ii) site specificity as to the particular chemical factors limiting tree growth. For example, Weetman and Webber (1972), working with two mature spruce-dominated stands in Quebec, identified calcium as a potential problem with respect to site improvishment, and they considered nitrogen removals to be insignificant. Boyle and Ek (1972), working on a 45 year old trembling aspen stand in Wisconsin, also considered calcium and magnesum removal to be a potential problem. However, they calculated that the amounts of nitrogen, phosphorus, and potassium in the plant-exploitable soil compartments were sufficient for at least five whole-tree rotations on their site. On the other hand, Norton and Young (1976), in a calculated budget for a mature softwood stand in Maine, concluded that whole-tree harvest removals of nitrogen, phosphorus, potassium, and sulfur were of sufficient significance to require subsequent fertilization treatments to avoid site deterioration. Similarly, White (1974), in a study of short-rotation cottonwood stands on alluvial sites in Alabama, concluded that biomass removals of nitrogen, phosphorus, and potassium might be of importance, whereas calcium and magnesium removals were not. Obviously, there is a high degree of species, age, site, and even regional differences as to the ecological effects of the removal of quantities of particular nutrients with harvested biomass.

The purpose of this report is to examine the potential effects of nutrient removals via intensive forest harvests on future site productivity. This will be done by presenting literature reviews (relevant to north temperate or boreal forests) of i) nutrient removals via forest harvest, ii) nutrient quantities in the total and plant-exploitable pools, iii) the major nutrient inputs via precipitation, dry deposition, weathering, and N_2 fixation, and iv) the net fluxes of nutrients (i.e., total inputs minus total outputs) from undisturbed stands, and also from stands affected by cutting, fire, or other disturbances. These data will then serve as the basis for simple calculations which evaluate the nutrient removals via intensive harvests of certain short, medium, or long-rotation hardwood or softwood stands, relative to: i) calculated total inputs to the site over a 100 year period, ii) calculated net fluxes over the same time period, and iii) the quantities of nutrients in the total and plant-exploitable soil pools. To limit the scope of this latter section, the sample calculations will be made for northeastern North American forest types, and the soils data will be representative of sites found in central Nova Scotia.

2. BIOMASS AND NUTRIENT STANDING CROPS OF FORESTS

Table 1 summarizes data describing the above-ground standing crops of biomass and nutrients of forest communities, both natural and artificial (plantations), and encompassing a

broad range of ages. These are thus equivalent to the maximum biomass yields and associated nutrient removals which could be realized from whole-tree harvests of these stands (actually, the efficiencies of biomass removal are generally less than 100%, even in a whole-tree clear-cut. For example, Hornbeck (1977) assumed a removal efficiency of 80% in his calculations of nutrient and biomass removals in the whole-tree clear-cutting of a northern hardwoods stand).

In following the scope of this review, most examples are pertinent to north temperate or boreal forest types. Also included in Table 1, for the sake of comparison, are data relevant to the standing crops of biomass and nutrients for a range of annual agricultural crops.

Consideration of the complex array of data assembled in this table clarifies a number of points. Most important, it is obvious that there is tremendous variation between sites, species, and stand age in the standing crops of biomass and nutrients. Other factors, such as stand history (particularly as it relates to patterns of natural disturbance or silviculture) may also be of significance. Variation between studies in methods of estimating biomass or in chemical analytical techniques may also have contributed to some of this variation in Table 1, and in other data presented elsewhere in this review.

The site effect can be illustrated by the data of Wood et al. (1977) for two three-year old plantations of Plantanus occidentalis, where above-ground biomass varied by 49%, nitrogen 72%, phosphorus 119%, potassium 152%, calcium 15%, and magnesium 43% (Table 2). Similarly, Ovington's (1962) data for two 47-year old plantations of Picea abies indicate site variations of 88% for biomass, 113% for nitrogen, 122% for phosphorus, 40% for potassium, 139% for calcium and 118% for magnesium (Table 2). Obviously, the site effect is of great importance and must be taken into account when predicting the uptake, or harvest removals of nutrients by tree crops. Note also that regional differences in these parameters can be even more significant than site differences within a region. For example, softwood stands of similar ages would be expected to differ considerably between high-rainfall coastal forests of the Pacific northwest, and moderate-rainfall coastal forests of the northeast. Most of these differences in biomass and nutrient standing crops would result from differences in relative growth rates, as influenced by climate, and not from effects related to different tree species on the sites.

Within particular sites, different species of trees also vary greatly with respect to growth rates and nutrient contents. This phenomenon is illustrated by the data of Alban et al. (1978), who compared the standing crops of biomass and nutrients in adjacent 40-year-old plantations of Pinus resinosa, Pinus banksiana, Picea glauca, and Populus tremuloides - P. grandidentata, growing in a fine sandy-loam soil in Minnesota (Table 3). Among these species, above-ground biomass varied from 141 to 199 MT ha^{-1}, nitrogen from 102 to 199 kg ha^{-1}, phosphorus from 25 to 57 kg ha^{-1}, potassium from 97 to 287 kg ha^{-1}, calcium 199 to 848 kg ha^{-1}, and magnesium from 40 to 58 kg ha^{-1}. Obviously, this species effect is of great importance, and must be taken into account when predicting the uptake or harvest removals of nutrients by various tree crops on a particular site (Alban (1979), for a more complete discussion of this topic).

The third major factor which strongly influences the biomass and nutrient contents of forests is stand age which, in modern forestry, can range from only one year on some

sites, to hundreds of years at the time of harvest. This effect is illustrated in Fig. 1 for Populus deltoides which, for six plantations ranging in age from 1 to 20 years, shows almost linear increases in standing crops over the time period considered. Note that these trends do not persist indefinitely, and with time the rates of net accumulation of both biomass and nutrients should decline in older stands. These decreases in rates of accumulation are illustrated over the medium-term by the data of Ovington (1959), who examined the process in a series of nine plantations of Pinus sylvestris, which varied in age from 7 to 55 years (Fig. 2). This process is also discussed for longer-term successional time periods in northeastern hardwood forests by Bormann and Likens (1979). The model of forest growth presented by these authors indicates that, in the absence of catastrophic disturbance, moderate declines in biomass (and presumably nutrient standing crop) would occur in overmature forests relative to moderate-aged forests, due to a shifting mosaic of microsuccession which occurs as individual trees are killed or senesce and die, producing gaps in the forest canopy which are occupied by younger trees of lower standing crops. Thus, stand age is another significant factor which must be considered when predicting the uptake or harvest of nutrients by a tree crop on a particular site.

In summary, it must be concluded that because of the tremendous variations in biomass and nutrient standing crops, due to the factors cited above, it is difficult to generalize these characteristics for broad forest categories (e.g., for "average" short, medium, or long-rotation hardwood or softwood forests). Thus, there is a high degree of site, regional, and tree species differences that must be considered when evaluating the removals of biomass or nutrients during forest harvests.

Table 4 summarizes data describing the standing crops (of biomass and nutrients) in a wide range of forest communities, both above-ground and in some cases, below-ground. In addition, the above-ground data have been compartmented into standing crop values relevant to contents in the merchantable boles of these forests, and into total above-ground contents. These data are equivalent to the biomass and nutrient contents of these forests that are potentially available to be harvested by conventional, whole-tree, or complete-tree clear-cutting.

Once again, it is readily observed that these data are highly variable between stands, due to differences in such parameters as site, region, tree species, forest age, and stand history. Thus, there is a high degree of stand specificity in the standing crops of biomass and nutrient, and hence potential removals of these via the various types of clear-cut harvest. It is therefore difficult to generalize about these removals for broad forest categories.

For all stands, it is apparent that there are increments in biomass removal in the calculated whole-tree or complete-tree harvests, relative to conventional removals. However, in all cases, the increments in nutrient removals are larger, and frequently much larger, than those for biomass. Thus, the increases in yields of biomass by the more intensive harvest methods would be obtained at the expense of much larger nutrient removals from the various forests stands. In some forest stands, these accelerated rates of removal of the nutrient capital of the site could be of ecological significance, if the enhanced removals were large relative to the amounts in the soil, or were larger

than rates of net input to the watershed over the stand rotation period. If this were true, then we could expect that the site would eventually become degraded with respect to its soil nutrient pool, and that future yields could be lowered as a result of this nutrient impoverishment. In the following sections we will examine the sizes of the major residual pools of nutrients, and the magnitudes of other flux components (i.e., inputs to, and outputs from the watershed), in order to assess this potential problem.

3. NUTRIENT POOLS IN FOREST SOILS

Table 5 illustrates data for the nutrient contents of the forest floors (i.e., litter, duff, and humus) and mineral soils over a range of forest types. Depending on the particular study, the data illustrate values for "total" amounts (i.e., acid digests), and "available" amounts (usually measured via soluble fractions for nitrogen (as NO_3-N plus NH_4-N), as weak acid-soluble for phosphorus (as PO_4-P), and as exchangeable ions in ammonium acetate for potassium, calcium, and magnesium).

The high site-to-site variation in Table 5 can be attributed to several factors, some of which undoubtedly act together. These include: i) real differences in soil fertility, due to differences in soil mineralogy, texture, and organic matter content, ii) differences in the depths of soil that were sampled (which in most studies reflected different plant-exploitable depths, which could vary according to such factors as the rooting depths of particular tree species on the site, the height of the water table, the presence of an impermeable hardpan or clay layer, etc.), and iii) differences in the analytical techniques that were used to measure the nutrient contents. This latter factor would be of particular significance in the measurement of the "available" or "exchangeable" fractions of the soil nutrient pool, as the chemical techniques for these measurements are not always standardized, among many studies.

In general, however, the amounts of the various nutrients in the total soil pools were large relative to the above-ground tree contents in the various studies of mature forests that were reviewed, while the amounts in the available or exchangeable pools were frequently similar to, or smaller than the amounts in the above-ground biomass. These relative fractions will be discussed in more detail in section 7 of this report.

4. NUTRIENT INPUTS TO FORESTS

Inputs of nutrients to forests occur mainly via four principal routes. These are precipitation, dry deposition, weathering, and nitrogen (N_2) fixation. These processes are discussed in the following pages.

a) Precipitation Inputs

Data relevant to inputs of nutrients with precipitation are summarized in Table 6. Variation in these nutrient inputs between the various sites likely reflects many factors. Of significance, would be differences in the amounts of precipitation that are received at different locales. In general, high precipitation sites have higher nutrient inputs via this route than do low precipitation sites (although this may be offset by more rapid rates of flushing). For some nutrients (particularly P), problems may exist with respect to errors inherent in the collection, preservation, and analysis of samples.

Other factors that influence the chemical composition of precipitation

may be of significance in some areas. For example, sites close to seashores may have precipitation inputs that are chemically influenced by marine aerosols, especially sodium and chloride, but also sulfate, magnesium, and other ions, although to a much lesser extent. Similarly, areas subject to large quantities of windblown dusts from agricultural fields may be influenced by this source, particularly with respect to potassium, calcium, magnesium, and phosphorus.

In addition, forested sites near large urban areas frequently receive relatively large precipitation inputs of NO_3-N, NH_4-N, and SO_4-S. these enhanced nutrient depositions are largely related to anthropogenic emissions of certain pollutants to the atmosphere. For example, large emissions of gaseous oxides of nitrogen (NO_x), primarily from internal combustion engines and power plants, may result in elevated atmospheric concentrations of these gases. These are oxidized in the atmosphere to NO_3^-, which may combine with NH_4^+ or some other atmospheric cation to form a neutral salt particulate. This may later serve as a condensation nucleus for a raindrop or snowflake, and be rained out of the atmosphere, or it may be washed out of the atmosphere by rainwater originating from clouds higher up. Similarly, gaseous sulfur dioxide is emitted in large quantities by coal and oil-fired power plants, sulfide metal smelters, and other industries. This SO_2 is oxidized photochemically and catalytically to sulfate in the atmosphere, where it may combine with ammonium or other cations to form a neutral salt or, if atmospheric cations are in short supply, it may exist as sulphuric acid. These are then available for deposition with precipitation as either rainout or washout, as previously described. Ammonia is also emitted to the atmosphere by anthropogenic sources, particularly by certain chemical industries and animal feedlots.

Overall, however, the site-to-site variations in nutrient inputs via precipitation are not overly large, and it is reasonable to calculate "typical" values for the array of north temperate sites (Table 6.) These calculations indicate mean precipitation inputs of ca. 6 kg ha^{-1} yr^{-1} nitrogen, 0.4 kg ha^{-1} yr^{-1} phosphorus, 1.7 kg ha^{-1} yr^{-1} potassium, 7.2 kg ha^{-1} yr^{-1} calcium, and 1.7 kg ha^{-1} yr^{-1} magnesium (Table 7).

b) Dry Deposition

Dry deposition of nutrients represents inputs of atmospheric particulates or gases, but occurring in the absence of precipitation. Included in this category would be the filtering of atmospheric particulates by forest canopies, the absorption of water- soluble gases onto moist surfaces, or direct gaseous uptakes via leaf stomata. Unfortunately, there are almost no quantitative measurements of nutrient inputs via dry deposition, although it appears that for some nutrients, particularly nitrogen and sulfur, the process is significant. For example, Likens et al. (1977) calculated dry inputs of fixed nitrogen at Hubbard Brook to be 14.9 kg ha^{-1} yr^{-1} compared with 5.8 kg ha^{-1} yr^{-1} via deposition with precipitation. Unfortunately, I am aware of no other data with which these can be compared. Although there are many measurements of atmospheric concentrations of NO_x gases, there are no measurements of their deposition velocities to vegetation surfaces (Unsworth 1977). However, likely approximations have been suggested (Grennfelt et al. 1980). The above also applies in general to NH_3, although it is likely that the dry deposition of this gas onto moist surfaces would be rapid, owing to its high solubility in water (Unsworth

1977). Similarly, Mayer and Ulrich (1974) calculated ratios of precipitation input:dry input of 13:6 for Ca, 4:5 for K, and 3:1 for Mg in a Fagus sylvatica stand. Miller et al. (1976) calculated analogous ratios of 3:4 for Ca, 3:7 for K, and 3:2 for Mg in a Pinus nigra forest in Scotland. In addition, it is known that the dry deposition of atmospheric sulfur onto moist surfaces can be very significant in SO_2-polluted areas, because of the high water-solubility of this gas (Unsworth 1977, Freedman and Hutchinson 1980a). It appears that atmospheric inputs of certain nutrients via dry deposition may prove to be quantitatively significant, particularly in relatively polluted areas where the concentrations of atmospheric gases of nitrogen and sulfur may be high, and possibly also in areas having high amounts of suspended particulates. However, much more work is required before these inputs can be reliably quantified.

c) Weathering

Weathering refers to nutrient release from bedrock or soil minerals, whereby nutrients bound as insoluble minerals are made water-soluble (and hence potentially available for plant uptake) by various chemical processes, such as oxidation, hydration, or carbonation. In general, the release of nutrients by weathering processes is highly variable between sites, and is strongly dependent on the primary mineralogy of the bedrock or soil parent material. Soft carbonaceous rocks, such as limestone or dolomite, weather at relatively higher rates in moist climates, and thus release minerals faster for plant uptake, as compared with hard, siliceous rocks, such as granites or gneisses. However, few good quantitative estimates of weathering rates exist, as the process is very difficult to measure by either direct or indirect techniques (Clayton 1979). These difficulties must be borne in mind when considering the data that follows.

Table 8 summarizes data from several studies, relevant to rates of weathering in forested watersheds. Nitrogen, which is not a constituent of most primary minerals, is not released in significant quantities by weathering processes. The two studies which included data on phosphorus release, indicate rates of ca. 0.6 kg ha^{-1} yr^{-1}. The release of potassium, calcium, and magnesium varied greatly between studies, depending on the nature of the primary minerals being weathered. Potassium release averaged ca. 5 kg ha^{-1} yr^{-1}, calcium averaged 18 kg ha^{-1} yr^{-1}, and magnesium averaged ca. 5 kg ha^{-1} yr^{-1}. The data of Art et al. (1974) were omitted from these calculations, as they refer to very depauperate quartzitic soils of an offshore island.

d) Nitrogen Fixation

The fixation of atmospheric nitrogen (N_2) is a biological process, occurring by the action of various micro-organisms via the enzyme nitrogenase. These micro-organisms differ taxonomically and ecologically, and include bacteria, actinomycetes, blue-green algae, or other micro-organisms. Some are free-living, and others live in associations with higher plants that range from loose rhizosphere associations, to symbiotic occurrences in root nodules (Wollum and Davey 1975; Postgate 1978; Davey and Wollum 1979; Jurgensen et al. 1979a).

Table 9 summarizes data illustrating rates of N_2 fixation in a variety of north temperate forest types. The tremendous range exhibited reflects the fact that some forests, dominated by trees or shrubs having symbiotic associations with N_2-fixing micro-organisms, have very high rates of fixation. For example, rates of fixation of up to

320 kg ha^{-1} yr^{-1} have been measured in an Alnus rubra stand in the Pacific northwest (Wollum and Davey 1975).

Because of the variation in the data, it probably would not be useful to calculate an "average" figure for N_2-fixation. However, Soderlund and Svenson (1976) have estimated that some 40 x 10^9 kg of N are fixed per year in the world's forests (accounting for ca. 29% of terrestrial biological N_2 fixation, and ca. 21% of total terrestrial N_2 fixation). If this estimate is standardized with Odum's (1971) figure of 39 x 10^6 km^2 of forest area on earth, then one can calculate a global mean rate of forest N_2 fixation of ca. 10 kg N ha^{-1} yr^{-1}.

Rotting wood on the forest floor is an important microsite for N_2 fixation, especially in forests having relatively acidic forest floors, which inhibit the growth of bacteria, blue-green algae, and actinomycetes (e.g., Jones et al. 1974; Bormann et al. 1977; Larsen et al. 1978; Likens et al., 1978; Bormann and Likens, 1979; Jurgensen et al., 1979 a,b). Bearing in mind the significance of rotting wood as a site for N_2 fixation, it seems that another problem which could arise indirectly from whole-tree or complete tree harvests might be a lack of these microsites, as these intensive harvest techniques leave relatively little slash or debris behind on the site.

Note also that some of this fixation of atmospheric N_2 may be offset by nitrogen losses by the denitrification of nitrate by microbiological processes which produce gaseous NO_x or N_2. Unfortunately, the process of denitrification has not yet been well established or quantified for forests. The data of Likens et al., (1978) for Hubbard Brook refer to "net fixation" (14 kg ha^{-1} yr^{-1}), i.e., N_2 fixation minus denitrification.

5. NET FLUX OF NUTRIENTS FROM FORESTS

The most significant output of nutrients from undisturbed forests occurs via streamwater or groundwater losses of suspended or soluble materials. In general, "the soils of a river basin govern the quantity, and the rocks the quality of the solids [i.e., suspended and soluble] in the water" (Viro 1953). Disturbance of forested watersheds is another key factor that influences the quantity and quality of nutrient losses via streamwater. This is dealt with in the next section.

Data will not be presented here that are directly relevant to streamwater losses of nutrients. However, Table 10 presents data for a variety of north temperate forested watersheds describing the net fluxes of nutrients, i.e., total inputs (usually measured via precipitation only) minus total outputs (usually measured via either streamwater or groundwater losses). If net flux values for a watershed are positive, then the watershed is accumulating the nutrient over time. Conversely, if the net flux is negative, then the watershed is suffering a net nutrient depletion.

From the data of Table 10, we can calculate a "typical" net flux for hard-bedrock watersheds (i.e., granitic and gneissic) of ca. +7 kg N ha^{-1} yr^{-1}, +0.3 kg P ha^{-1} yr^{-1}, -0.6 kg K ha^{-1} yr^{-1}, -7 kg Ca ha^{-1} yr^{-1}, and -2 kg Mg ha^{-1} yr^{-1}. On watersheds situated on limestone or dolomite bedrock or till, we would expect that the negative net fluxes of calcium and magnesium would be more than an order of magnitude higher (c.f. data of Henderson et al. 1977b included in Table 10).

6. FOREST DISTURBANCE AND NET FLUX

It is well established that large-scale disturbances of forested ecosystems lead to accelerated losses of nutrients from their watersheds, and thus cause losses of the nutrient capital from the site. The disturbances that are considered here are forest fire, forest harvest, and briefly, pollutant interactions, such as acidic precipitation.

a) Effects of Forest Fires on Nutrient Losses

The burning of forests can lead to nutrient losses via three principal mechanisms. These are: volatization losses to the atmosphere, and streamwater losses via accelerated rates of erosion, or leaching.

Losses of nitrogen to the atmosphere occur via the volatilization of organically-bound nitrogen in either soils or vegetation, with the process being particularly rapid at higher combustion temperatures (Knight 1966; Grier 1975; Evans and Allen 1971; De Bano et al. 1979; Dunn et al. 1979; Raison 1979). The mechanism of nitrogen volatilization is not yet firmly established, and may, in fact, differ for burns of different intensities. Postulated mechanisms include the loss of nitrogen as NH_3 (Hosking 1938), loss as N_2 (DeBell and Ralston 1970), or loss as NO_x (Sandburg et al. 1979). The actual percentage loss to the atmosphere of the total nitrogen in the fuel depends on the characteristics of the burn, including moisture content of the fuel (e.g., De Bano 1979; Dunn et al. 1979, in Table 11), and the temperature of the combustion (e.g, Knight 1966, in Table 11). Under moderate burn conditions, nitrogen losses as low as 10% are reported, while high temperature burns of dry fuels report nitrogen losses of up to 67% (Table 11). Thus, fire can cause very large losses of nitrogen from forested sites, especially if the forest floor burns in addition to the above-ground vegetation. For example, three studies reporting on nitrogen losses to the atmosphere during wildfires in coniferous forests described losses of 855 kg N ha (Grier 1975), 580 kg ha (Kimmins and Feller 1976), and 320 kg ha (Viro 1974). These wildfire losses are equivalent to, or greater than, the potential whole-tree harvest removals from most mature coniferous forests.

Atmospheric losses of other nutrients as a result of forest fire have also been reported, although they are generally much less than those of nitrogen (Table 11). These occur mainly via convective losses of particulates rather than by volatilization.

Interestingly, in spite of the considerable losses of nitrogen and other nutrients to the atmosphere following forest fires, indicating lowered quantities stored on the site, it is frequently (but not always) reported that there are short-term increases in post-burn nutrient availabilities in soils. This allows in some cases for the vigorous regrowth by surviving or invading species (e.g., Vlamis et al. 1955; Ahlgren and Ahlgren 1960; Knight 1966; Smith 1970; Wagle and Kitchen 1972; Boyle 1973; Viro 1974; St. John and Rundel 1976; Smith and James 1978; De Bano et al. 1979; Dunn et al. 1979; Raison, 1979; Stark, 1980a.)

The burning of forests also leads to accelerated rates of nutrient loss from watersheds by the erosion of suspended particulates, or by the leaching of soluble ions. The relative degree of effect depends on many factors, including the intensity of the burn, and various site factors, such as slope, soil type, etc. Data summarizing the results of several studies investigating this phenomenon are presented in Table 12 (the subject has also been reviewed recently

by Tiedemann et al. 1979). Most of these studies document the syndrome of accelerated nutrient loss, and they show that this can occur at rates that are similar to or greater than those observed following the clear-cut logging of forested sites (next section).

b) Effects of Forest Harvest on Nutrient Losses

In some situations, the harvesting of forests can lead to significant losses of soils and nutrients from watersheds by erosion and leaching. Because of the potential ecological significance of this problem, due to losses in site fertility, siltation of water bodies, and destruction of freshwater wildlife habitats, this process has been studied fairly intensively, and several recent reviews have been published (e.g., Megahan 1972; Rice et al. 1972; Sopper 1975; Patric 1976; Corbett et al. 1978; Hornbeck and Ursic 1979; Martin and Pierce 1979; McColl and Grigall 1979; White and Harvey 1979; see also Table 13).

With regards to erosion from harvested forests, the conclusions of Rice et al. (1972) are enlightening: i) most logging activities increase the rates of erosion from forested lands, ii) erosion is spatially non-uniform on harvested sites, iii) initially high rates of sedimentation following disturbance are reduced rapidly, usually within two to five years, iv) landslides and creep are the most important erosional processes in mountainous areas, v) steep slopes are especially vulnerable, and vi) roadbuilding is a very important factor in causing erosion from forested lands. Most authors agree, however, that large erosional losses from watersheds do not necessarily have to occur after logging, if established guidelines for proper operational practices are followed. These practices should include: i) the proper planning of forest roads, ii) careful installation of culverts, iii) avoidance of stream crossings or of using streams as skidding trails, iv) leaving of buffer strips of uncut forest along watercourses, v) using skidding techniques that have minimal effects on the integrity of the forest floor (e.g., cable logging (Patric 1980)), vi) allowing or encouraging rapid vegetation regrowth on the site to speed the reestablishment of biological moderation of erosion, or, ultimately, vii) decisions to leave hypersensitive sites uncut.

Table 14 summarizes data from studies that documented increased discharges of sediments from logged watersheds. In general, results from the various studies are highly variable, due to the great differences between watersheds in susceptibility to erosion. It can be concluded, however, that although erosion can undoubtedly contribute to significant losses of soils and nutrients from certain susceptible watersheds, the losses can be minimized by the use of proper precautions during the road-construction, harvesting, and regeneration phases of the logging operation. However, it could also be concluded that intensive harvest techniques (such as complete-tree harvesting) which would severely disturb the soil surface during stump and root removals, could cause severe erosion on some sites.

A large number of studies have examined the leaching of soluble nutrients from logged watersheds. Leaching results in increased concentrations of some nutrients in streamwater, and therefore increased losses from the site. Of particular concern are the losses of nitrogen, mainly as soluble nitrate. Elevated concentrations of nitrate in streamwater draining certain logged areas probably are the result of several factors. These include: i) increases in the rates of mineralization of

organic matter (causing the release of a portion of the organically-based nitrogen as ammonium or nitrate), due to increased microbial activity resulting from a) warmer surface soils, b) an influx of organic matter into the soil, c) an increase in nutrient availability and d) decreased moisture stress (the latter two factors are related to a decline in the uptake of nutrients and water by higher plants following logging) (Cole and Gessel 1965; Likens et al. 1970; Piene 1974; Cole et al. 1975 Jurgensen et al. 1979b), and ii) an increase in the populations and activity of nitrifying bacteria following the logging of certain sites (Likens et al. 1970). Notably, this increase in the activity of nitrifiers does not appear to occur on all clear-cut sites (Reinhart 1973).

Table 15 summarizes data for the studies listed in Table 13, relevant to streamwater losses of nutrients from clear-cut watersheds. Once again, the highly variable site-to-site data indicate differences in susceptibility to nutrient losses via this route. The conclusions of Sopper (1975), in a recent review, may be relevant here: i) except for studies at the Hubbard Brook Experimental Forest (e.g., Likens et al. 1977, 1978; Bormann and Likens 1979), few studies have shown large increases in nutrient losses from harvested sites by this route, and ii) even after disturbance by logging, nutrient discharges by streamwater are generally low, relative to site nutrient capital, so that decreases in site productivity are not anticipated. Sopper (1975) also noted few effects of the silvicultural use of herbicides on nutrient losses by streamflow.

c) Other Disturbances

Several other local or regional disturbances also bear mentioning, as they may affect rates of nutrient cycling, or may increase nutrient losses from watersheds, and hence they could interact with possible effects of forest harvesting on these processes. The potential effects of acidic precipitation are especially significant because of the pervasive and regional nature of the phenomenon over large tracts of forested land, particularly in the northeast of North America.

Numerous authors have recently reported the results of field or laboratory experiments where plants were subjected to simulated "acid rains" in the form of mists or sprays (e.g., Wood and Bormann 1974, 1975; Abrahamsen et al. 1976; Fairfax and Lepp 1976; Ferenbach 1976; Evans et al. 1977; Galloway et al. 1978; Matziris and Nakos 1978; Jacobson 1980; Tukey 1980; Tveite and Abrahamsen 1980). In general, these authors find measurable acute effects at only very low solution pH's (i.e., pH <3. Notably, these pH's are much lower than those normally encountered in nature, and thus the acidities are unrealistically high. For example, the average annual pH of precipitation in Ontario is ca. 4.0 - 4.3, and in Nova Scotia ca. 4.0 - 4.6, although the pH of individual events may be lower (Dillon et al. 1977; Shaw 1979; Ogden 1980). In fact, it is notable that not a single incidence of acute injury to vegetation, resulting from a naturally-occurring acidic precipitation event, has been reported in the scientific literature!

Although acute toxicity to vegetation does not appear to be a problem with respect to acidic precipitation, the possibility of subacute, chronic effects does exist. These would result in growth decrements which would reduce yields, but would not be manifest in acute injuries. Such effects could result from several direct or indirect causes, such as accelerated base leaching from foliage, decreases

in photosynthesis or increases in respiration, changes in nutrient availability due to biological or chemical effects in soils, or other factors (the potential mechanisms are summarized in various sources, including Tamm 1976; Tamm and Cowling 1976; Galloway et al. 1978; Wood 1979; Hutchinson and Havas 1980). Several studies have attempted to demonstrate decreases in the growth rates of forests using dendrochronological techniques. These studies compared either current growth rates to past rates, or growth rates between areas experiencing acidic precipitation with areas receiving circumneutral precipitation. Notably, none of these studies have conclusively documented decreases in forest productivity that could be attributed to the effects of acidic precipitation (e.g., Jonsson and Sundberg 1972; Abrahamsen et al. 1976, 1977; Cogbill 1977). However, this apparent lack of effect could be an anomaly of the fact that the spatial and temporal heterogeneity of forest growth means that relatively small changes in forest productivity cannot be detected (i.e., even relative growth decrements as large as, for example, 5-10% cannot be detected in an ecosystem as heterogenous as a forest, using these methods).

It should also be noted that many regions in Canada (particularly in the western provinces), as well as other areas in the world, are known to have sulfur-deficient soils. This is especially true for many agricultural soils, which may receive large quantities of nitrogen, phosphorus, and potassium fertilizers (e.g. Jordan and Ensminger 1958; Coleman 1966; Cowling and Jones 1970; Beaton et al. 1976). In these cases sulfur may be a limiting factor, and sulfur-containing precipitation may actually be ameliorative to these soils.

As with vegetation, few chemical or biological changes have been found in soils experimentally receiving "rainfall" having acidities that are comparable to that of naturally-occurring precipitation. One possible exception is the acceleration of leaching of basic cations (e.g., calcium, magnesium, or potassium) from experimental soil lysimeters receiving solutions of various pH. With some soils, even moderately acidic solutions (e.g., pH of ca. 4.0) will increase base loss (Oden and Anderssen 1971; Overrein 1972; Fairfax and Lepp 1976; Tamm et al. 1976; Abrahamsen et al. 1976, 1977). This accelerated base leaching could possibly be of longer-term significance in the nutrient impoverishment and acidification of certain sensitive soils, in particular free-draining, poorly-buffered soils having pH's of ca. 4-6, with low anion-exchange capacity, and located in regions receiving relatively large amounts of precipitation (e.g., certain brunisols). These relatively sensitive soils are widespread over parts of northeastern North America, as are the non-sensitive north temperate soil types, such as well-buffered calcareous soils having pH's above 6 (luvisols), or well-buffered acidic soils having pH's below 3.5-4.0 (e.g., podsols) (after Bache 1980; Johnsen and Freedman 1980; Petersen 1980; Schnitzer 1980; Seip and Freedman 1980; Wiklander 1980). Significantly though, there is no documented evidence that forest or agricultural soils have been acidified or significantly impoverished as a result of acidic precipitation occurring at pH's typical of those observed in the field. Thus, the problem is a potential, longer-term one (Johnsen and Freedman 1980). However, if the problem does prove to be a real one, then it would be of great ecological and economic significance, because of the tremendous areas of forested land that would be affected.

Other disturbances have also been linked to changes in the rates of nutrient cycling in forests. For example, decreased rates of litter decomposition and other microbial processes have been observed in metal-contaminated forest soils close to polluting smelters, and this undoubtedly slows nutrient cycling in the affected stands (Tyler 1974, 1975 a,b, 1976; Strojan, 1978; Freedman and Hutchinson 1980 a,b). These problems are, however, localized to the vicinities of the smelters. Thus, they are not of widespread significance, and would not interact with the effects of intensive forest harvest over large areas.

7. EVALUATION OF NUTRIENT REMOVALS BY FOREST HARVEST.

In this section, simple calculations will be presented which attempt to evaluate the ecological significance of nutrient removals with intensively-harvested biomass. To this end, harvest removals for selected stands of various rotation lengths and harvest methods will be compared with i) calculated nutrient inputs (over a 100-year period) via precipitation, weathering, and N_2 fixation, ii) with calculated net fluxes over the same period, and iii) with amounts in the total and plant-available soil pools. It must be stressed that, because of the wide site-to-site variations that are found in the magnitudes of the various nutrient pools and fluxes, only limited confidence can be placed on the calculated "average" data for these parameters. This also applies to the data relevant to soil pools, which in most cases, refer to an average for hardwood or softwood sites in central Nova Scotia, calculated using the data of Freedman et al. 1980b). The data relevant to harvest removals are from selected, "typical" stands of various ages, all occurring in northeastern North America (i.e., no attempt was made to calculate "average" nutrient removals for short, medium, or long-rotation forests).

In addition, no attempt was made in these simple calculations to account for changes in the rates of influx or efflux of nutrients from sites that might be caused or changed by clear-cut logging (e.g., increased leaching or erosion, changes in the rates of N^2 fixation or denitrification, etc.). This was done because: i) some of the negative effects can be minimized by careful planning and execution of harvesting operations, ii) the data are much too variable and site-specific to make generalizations (e.g., accelerated leaching losses), or iii) not enough information is currently available to make generalizations (e.g., N_2 fixation or denitrification). Note, however, that these effects would be of special significance for the shorter-rotation stands, as disturbances of these would be much more frequent.

a) Short-Rotation Plantations

Tables 16 and 17 summarize data relevant to calculated nutrient removals over a 100-year period by consecutive 1-year rotations of a hybrid Populus plantation, and 7-year rotations of a Populus deltoides plantation, expressed relative to calculated rates of nutrient inputs and net fluxes over the same time period, and to the soil nutrient contents of a "good" hardwood soil in central Nova Scotia.

The data for the Populus hybrid (Table 16) indicate that, with 100 consecutive whole-tree rotations of this nutrient-demanding crop, severe impoverishments of the site nutrient capital would occur. For example, removals of nitrogen would be about 5.4 times the total inputs over the 100-year period, phosphorus 13,

potassium 6.6, calcium 2.3, and magnesium 2.4 times. Similarly, the nitrogen removals would exceed the initially positive net flux by 12 times, and phosphorus by 43 times, while the pre-existing negative net fluxes of potassium, calcium, and magnesium would be accentuated by factors of 73, 8.3 and 8.0 times, respectively. In addition, the pre-existing soil pools of total nitrogen, phosphorus, potassium, calcium, and magnesium would be depleted by about 63, 38, 18, 43, and 18 %, respectively.

However, the "available" soil pools would be depleted by much larger factors, i.e., by factors of 108 for nitrogen, 5.2 for phosphorus, 31 for potassium, 20 for calcium, and 29 for magnesium. Thus, one could reach very different conclusions about the effects of removals of nutrients via intensive forest harvests. depending on whether the nutrient removals were expressed relative to the total or to the available soil pools for the various nutrients. The total pools represent the gross soil nutrient capital of the site, although most of it is present in a chemical form which is unexploitable by higher plants, until it is mineralized and made plant-available by either inorganic processes or by the actions of soil microorganisms. On the other hand, the available soil pools, although much smaller in quantity than the total soil pools, are relatively ephemeral, (i.e., they have large inputs and outputs relative to the sizes of the available pools themselves), in that the turnover times are rather rapid. For example, at the Hubbard Brook northern hardwoods forest, the available soil pol of nitrogen had a turnover time of only 1.2 years, while the turnover time of available calcium was 7 years (calculated from Likens et al. 1977; Bormann and Likens 1979). Thus, it may not be of great ecological significance that apparent depletions of available nutrient pools are calculated, since they may be rapidly replenished by mineralization of some fraction of the unavailable pools. In fact, it is frequently observed that short-term increases in the amounts of available nutrients occur in logged or burned areas (discussed in sections 7a and b). In addition, because of uncertainty over the ecological meaning of current measurements of nutrient availability (i.e., Do the various chemical extractions actually provide a measure of available nutrients that is quantitatively similar to that perceived by plants?), and because of poor standardization of techniques, it is frequently difficult to interpret data describing nutrient availability, or to compare different studies (see Black et al. 1965; and Allen et al. 1974 and for a more complete discussion of this problem). Overall, it seems likely that an ecologically-meaningful measure of soil nutrient pools, with which nutrient removals can be compared, would lie between the total and available measurements, but (in the opinion of the author) possibly leaning towards the total measurements. This would be particularly true for long forest rotations.

In any event, it appears obvious that, because the nutrient removals in intensively-harvested short-rotation plantations are large relative to the magnitudes of the total inputs, to net fluxes, and to the soil nutrient pools, the use of such an intensive silvicultural system on this site would have to be accompanied by nutrient restoration by fertilization with all of the described nutrients. Indeed, operational trials involving agro-forestry tree crops are heavily fertilized, so that yields can be both maximized and sustained.

The calculations relevant to a 7-year rotation of Populus deltoides are summarized in Table 17. These data indicate much lower nutrient removals over an equivalent 100-year period than those calculated for the 1-year Populus hybrid rotation. However, the nutrient removals with harvested biomass still appear to be significant. The nutrient removals by the whole-tree-harvest would exceed the calculated total inputs by factors of 1.9 for nitrogen, 4.1 for phosphorus, 3.8 for potassium, 2.0 for calcium, and 0.8 for magnesium, while the calculated pre-existing positive net fluxes for nitrogen and phosphorus would be exceeded by factors of 4.3 for nitrogen, and 13.8 for phosphorus, and the negative net fluxes of potassium, calcium, and magnesium would be accentuated by factors of 42, 7.1 and 2.7, respectively. Whole-tree harvest nutrient removals would also deplete the soil quantities of total nitrogen, phosphorus, potassium, calcium, and magnesium by 22, 12, 10, 37, and 6%, respectively, and the available quantities of these nutrients by much larger amounts. In view of these data, it appears likely that these short-rotation harvests would require nutrient restoration by fertilization.

b) Medium-Length Rotations

Tables 18 and 19 summarize calculations relevant to the nutrient removals with intensively-harvested biomass by two medium-length rotations - one a 29-year rotation of intolerant hardwoods, and the other a 40-year rotation of a Pinus resinosa plantation. Both of these harvest treatments would result in substantially lower nutrient removals than those calculated for the short-rotation Populus plantations. For example, removals of nitrogen with whole-tree-harvested biomass from the 1-year Populus hybrid plantation were calculated as 8600 kg ha^{-1} 100 yr^{-1}, and 2986 kg ha^{-1} 100^{-1} yr from the 7-year Populus deltoides plantation. These compare with 817 kg ha^{-1} 100 yr^{-1} from the 29-year rotation of intolerant hardwoods, and 865 kg ha^{-1} 100 yr^{-1} from the 40-year plantation of Pinus resinosa (Tables 16, 17, 18 and 19).

These result in more moderate calculated depletions of site nutrient capitals in the medium-rotation stands. For example, with the 29-year rotation of an intolerant hardwood stand (Table 18), nutrient removals with whole-tree-harvested biomass would be 51% of the total inputs of nitrogen, 111% for phosphorus, 66% for potassium, 39% for calcium, and 15% for magnesium. Similarly, the nutrient removals with harvested biomass would be only 1.2 times the calculated pre-exisitng net flux for nitrogen, and 3.7 times that for phosphorus, while the negative net fluxes for potassium, calcium, and magnesium would be accentuated by factors of ca. 7.4, 1.4, and 0.5. respectively. Moderate depletions of the soil pools of total nitrogen, phosphorus, potassium, calcium, and magnesium would occur, amounting to about 9, 4, 2, 7, and 2% of the total, respectively, although the removals relative to the sizes of the available pools would be much larger. Observations similar to those noted above for the intolerant hardwood stand can also be made for the calculated 40-year rotation of Pinus resinosa (Table 19). Because the nutrient removals with intensively-harvested biomass are not large in comparison with total inputs, net fluxes, or soil pools, it appears unlikely that nutrient restoration by fertilization would be required, except perhaps over time periods of the order of centuries.

b) Longer Rotations

Tables 20 and 21 summarize calculations relevant to the nutrient removals with intensively-harvested

biomass for two longer rotations - one a 55-year rotation of tolerant northern hardwoods, the other a mature, about 100 year-old mixed-age stand of Picea rubens - Abies balsamea. Both of these harvest treatments would result in substantially lower nutrient removals than those calculated for the two short-rotation Populus plantations, although the removals are roughly comparable with those calculated for the medium-rotation stands. For example, removals of nitrogen with whole-tree-harvested biomass for the 1-year Populus hybrid plantation were calculated to be 8600 kg ha^{-1} 100 yr^{-1}, and 2986 kg ha^{-1} 100^{-1} for the 7-year Populus deltoides plantation. The analagous removals for the medium-rotation stands were 817 kg ha^{-1} 100 yr^{-1} for the 29-year rotation of intolerant hardwoods, and 865 kg ha^{-1} 100 yr^{-1} for the 40-year plantation of Pinus resinosa. These nitrogen removals compare with 675 kg ha^{-1} 100 yr^{-1} for a whole-tree clear-cut on a 55-year rotation of a tolerant northern hardwoods stand, and 239 kg ha^{-1} 100 yr^{-1} for a mixed-age Picea rubens - Abies balsamea stand (Tables 16 to 21).

These results imply moderate calculated depletions of site nutrient capitals in the longer-rotation stands. With an approximately 100-year rotation of the Picea rubens - Abies balsamea stand (Table 21), nutrient removals with whole-tree-harvested biomass would be only 15% of the total calculated inputs of nitrogen, 35% for phosphorus, 20% for potassium, 13% for calcium and 6% for magnesium. Similarly, the whole-tree harvest nutrient removals would only be 34% of the calculated positive net flux of nitrogen over the 100-year period, and 117% for phosphorus, while the negative net fluxes of potassium, calcium, and magnesium would be increased by factors of 2.2, 0.5, and 0.2, respectively. In addition, only small depletions of the soil pools of total nitrogen, phosphorus, potassium, calcium, and magnesium would occur, amounting to about 6.4, 2.8, 1.0, 5.9, and 2.1% of the total, respectively, although the available pools would be exceeded for most elements. Because these harvest removals appear to be small relative to the total inputs and net fluxes, and especially with respect to the total soil pools, it appears unlikely that nutrient restoration via fertilization or other treatments would be required, except perhaps over long time periods.

8. CONCLUSIONS

It is clear that the use of intensive harvest techniques, such as whole-tree or complete-tree clear-cutting, will produce substantially higher yields of biomass than would conventional bole-only clear-cutting of the same stand. However, these increases in the yield of biomass are accompanied by much larger increases in the removals of nutrients, because relatively nutrient-rich tissues such as foliage, twigs, and small branches are also removed from the site when intensive harvests are practiced. Thus, the short-term biomass gains are purchased at the longer-term expense of accelerated nutrient removals.

These nutrient removals can be further increased by severe disturbance of the site during the logging operation, via particulate losses by erosion or by soluble nutrient leaching into streams. Notably, nutrient losses by these mechanisms also occur following natural disturbances of forest soils (e.g., after wildfire), and frequently at higher rates than those observed after logging. Severe wildfires can also result in very substantial volatilization losses of

nitrogen, frequently occurring at rates that are higher than those that would occur by an intensive harvest of the same stand.

Simple calculations presented here indicate that, for short-rotation (i.e., 1-7 yr) Populus plantations, the nutrient removals with whole-tree-harvested biomass would result in a relatively rapid nutrient impoverishment, and thus this intensive, agroforestry type of site management must be accompanied by fertilization to restore nutrients and to allow sustained high productivities.

On the other hand, calculations relevant to medium or longer-length rotations indicate more moderate removals of nutrients with harvested biomass. These are generally less than the calculated inputs over a 100-year period, and are small relative to the sizes of the total soil nutrient pools (although they are large compared to the sizes of the relatively ephemeral available nutrient pools). Because only moderate depletions of the site nutrient capital are calculated to occur, it appears on the basis of these simple calculations that intensive harvests on medium or longer-length rotations might not result in declines of site productivity via nutrient impoverishment, except possibly after several consecutive rotations. However, due to variations and other uncertainties in many of the data upon which these calculations were based, these conclusions are tentative, and perhaps should not be taken at face value. Certainly, longer-term studies are required of the effects of intensive tree cropping on subsequent site productivity. These will require more site and regional-specific field studies, and further refining and field-testing of forest growth models (e.g., Aber et al. 1978, 1979; Kimmins et al. 1980).

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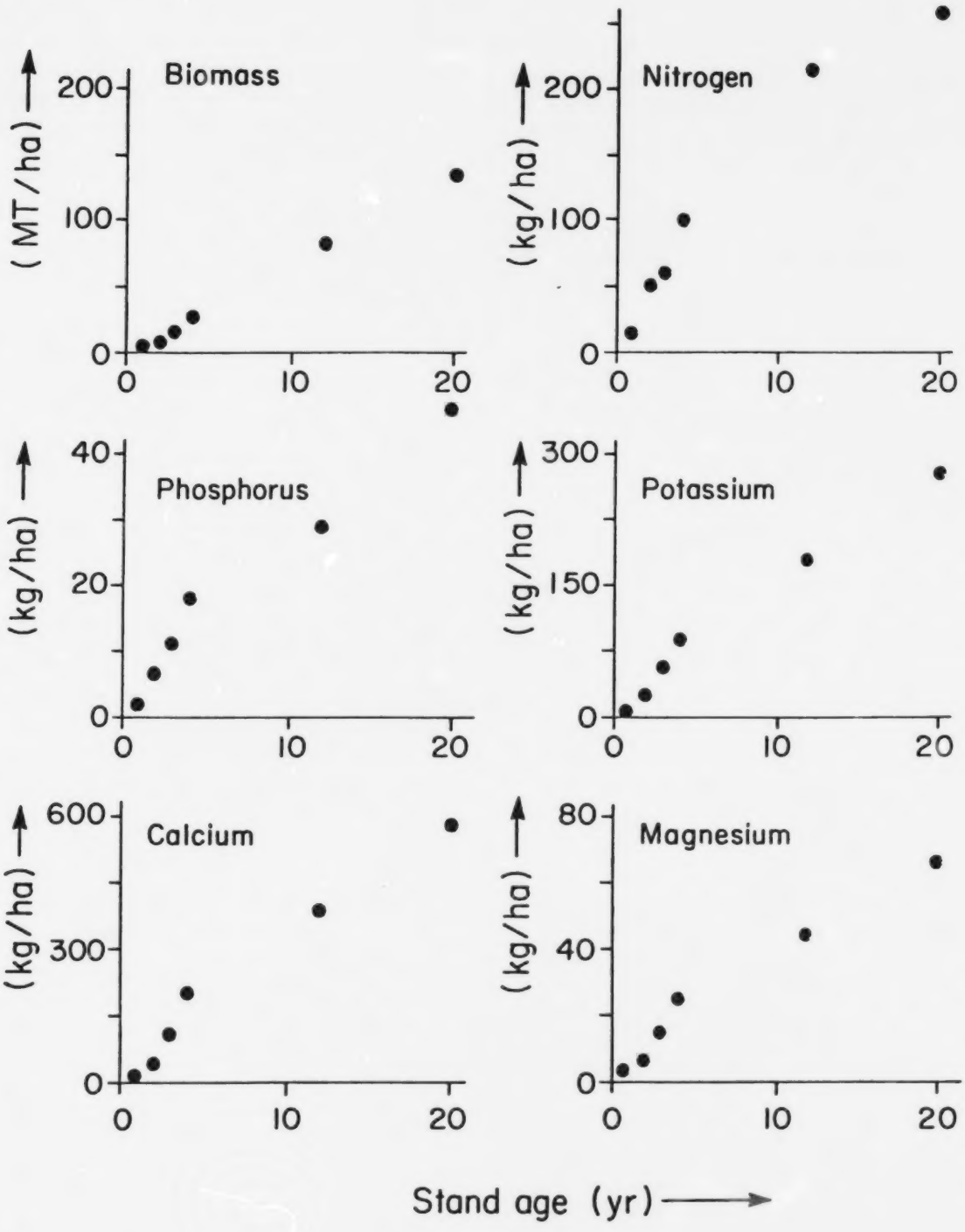

Fig. 1. The effects of stand age on the above-ground standing crops of biomass and nutrients in Populus deltoides plantations (after Hansen and Baker 1979).

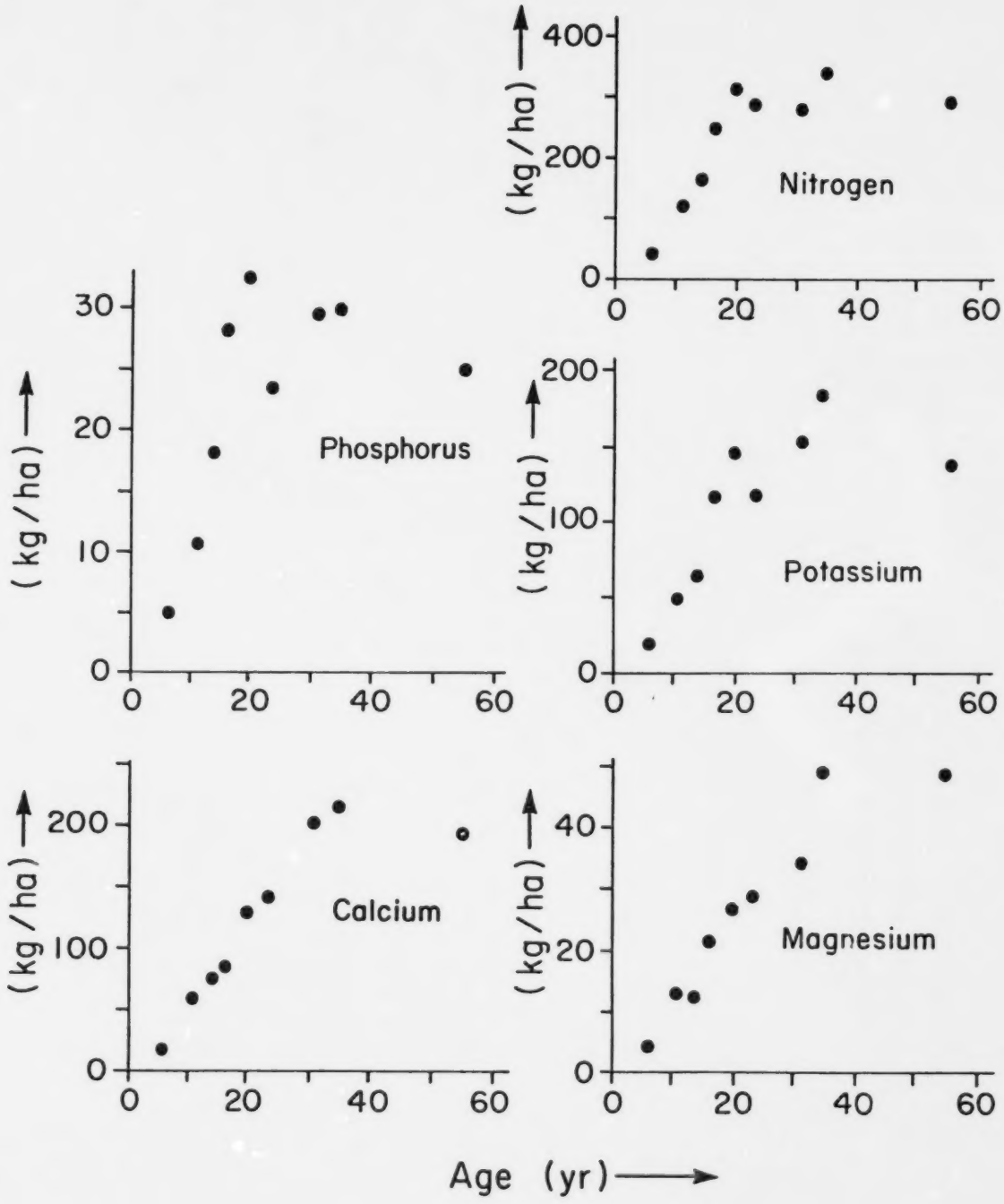

Fig. 2. The effects of stand age on the above-ground standing crops of nutrients in Pinus sylvestris plantations (after Ovington 1959a).

TABLE 1. Summary of literature relevant to the above-ground biomass (dry weight) and nutrient standing crop of a variety of forest types and agricultural crops. N = natural stand, P = plantation.

STAND	AGE	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Tropical (median)	mature	378	7260	241	2157	4005	437	Marion, 1979
Nothofagus truncata (N)	110	280	415	48.5	448	1211	123	Miller, 1963
Hardwoods (P)	50	-	-	71.7	311	1144	-	Rennie, 1955
Hardwoods (P)	100	-	-	124	556	2172	-	Rennie, 1955
Temperate Broadleaf (median)	mature	338	1085	73	463	1142	115	Marion, 1979
Mixed Hardwoods (mean) (N)	7-20	-	50	9	40	40	8	MacLean and Wein, 1977
Mixed Hardwoods (range) (N)	24-37	-	150-250	20-35	90-160	90-150	15-30	MacLean and Wein, 1977
Northern Hardwoods (N)	mature	111	278	22	-	368	-	Hornbeck and Kropelin, 1979
Northern Hardwoods (N)	55	-	351	34	155	383	36	Hornbeck, 1977; Likens et al., 1977.
Northern Hardwoods (N)	55	60.4	371	35	155	403	38	Whittaker et al., 1979
Coastal Hardwoods (N)	-	-	-	-	363	464	178	Art et al., 1974
Betula papyrifera-Acer rubrum Populus tremuloides (N)	29	79.8	237.2	32.1	127.9	282.5	29.4	Ribe, 1974
Acer rubrum - Fagus grandifolia Betula papyrifera (N)	90	202.7	483	-	-	541	-	Hornbeck, 1977
Acer rubrum (N)	18	37.2	164.9	23.6	86.3	201.5	20.6	Ribe, 1974

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Acer rubrum (N)	30	57.4	192.4	28.6	108.8	300.8	25.8	Ribe, 1974
Alnus incana (P)	22	111.1	640	56	128	584	39	Ovington, 1962
Alnus rubra (N)	34	210	589	37	99	299	111	Turner et al., 1976
Betula papyrifera (N)	39	131.4	332.6	39.7	167.5	277.9	39.9	Ribe, 1974
Betula verrucosa (P)	22	60.8	240	30	62	312	24	Ovington, 1962
Betula verrucosa (N)	24	62.2	188	14	78	233	24	Ovington and Madgwick, 1959b
Betula verrucosa (N)	55	164.0	391	27	154	497	46	Ovington and Madgwick, 1959b
Fagus sylvatica(N)	39	133.4	283	38	185	151	42	Ovington, 1962
Fagus sylvatica (N)	90	315	830	54.7	465	924	121	Nihlgard and Lindren, 1977
Fagus sylvatica (N)	90	324	1060	84.5	460	603	105	Nihlgard and Lindren, 1977, Nihlgard, 1972
Fagus sylvatica (N)	100	225	640	62	318	478	85	Nihlgard and Lindgren, 1977
Platanus occidentalis (P) (dormant season, leafless)	1	-	22.8	4.9	14.5	17.1	3.0	Blackmon, 1979
Platanus occidentalis (P) (dormant season, leafless)	2	-	36.0	7.7	23.1	25.7	4.7	Blackmon, 1979
Platanus occidentalis (P) (dormant season, leafless)	4	-	36.6	7.9	23.5	25.2	4.7	Blackmon, 1979
Platanus occidentalis (P)	3	9.2	52.3	9.6	20.8	45.7	16.7	Wood et al., 1977
Platanus occidentalis (P)	3	13.7	89.7	21.0	52.5	52.9	23.9	Wood et al., 1977
Populus (hybrid) (P)	1	4.6	62	12	91	55	13	Anderson, 1979

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Populus (hybrid) (P)	1	10.0	86	13	44	58	-	Hansen and Baker, 1979
Populus (hybrid) (P)	2	22.7	120	17	52	118	14	Hansen and Baker, 1979
Populus (hybrid) (P)	3	17.8	144	21	57	90	22	Hansen and Baker, 1979
Populus (hybrid) (P)	4	36.8	213	31	86	126	23	Hansen and Baker, 1979
Populus deltoides (P)	1	2.42	29.5	2.5	20.0	27.5	5.3	Baker and Blackmon, 1977
Populus deltoides (P)	1	1.6	14	2	7	9	2	Hansen and Baker, 1979
Populus deltoides (P)	2	7.8	50	7	25	45	7	Hansen and Baker, 1979
Populus deltoides (P)	3	15.0	62	11	52	120	16	Hansen and Baker, 1979
Populus deltoides (P)	4	26.9	101	18	92	203	25	Hansen and Baker, 1979
Populus deltoides (P)	12	80.6	214	29	173	384	45	Hansen and Baker, 1979
Populus deltoides (P)	20	136	256	47	277	588	66	Hansen and Baker, 1979
Populus deltoides ($\bar{x}$ of 8 stands) (P)	6-9	-	225	192	179	174	178	White, 1974
Populus tremuloides - Betula papyrifera (N)	45-50	46.6	206.6	21.4	107	441	42.8	Boyle and Ek, 1972
Populus tremuloides - P. grandidentata(P)	40	1668	368	46.5	287	848	57.6	Alban et al., 1978
Populus tremuloides (N)	45	58.0	195.0	18.0	93.7	327.3	28.0	Ribe, 1974
Prunus pensylvanica- Betula spp.(N)	4	7.1	52	4.3	22.6	19.6	2.3	Safford and Filip, 1974
Quercus-Carya (N)	-	-	405	-	-	830	-	Huff et al., 1978

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Quercus robur - Fraxinus excelsior(N)	114-160	294	947	64	493	1338	126	Duvigneaud and Denaeyer-De Smet 1967
Quercus petraea (P)	21	42.4	284	19	102	119	28	Ovington, 1962
Quercus robur (N)	47	128.3	369	32	223	246	41	Ovington, 1962
Softwoods (P)	50	-	-	74.1	343	652	-	Rennie, 1955
Softwoods (P)	100	-	-	101	578	1082	-	Rennie, 1955
Temperate Coniferous (median)	mature	291	664	47	263	717	-	Marion, 1979
Boreal Forest (median)	mature	129	447	50	291	488	108	Marion, 1979
Abies lasiocarpa - Tsuga heterophylla (N)	175	337	320	50	819	992	130	Turner and Singer, 1976
Larix decidua (P)	46	189.4	465	44	142	172	35	Ovington, 1962
Picea glauca-Abies lasiocarpa (N)	<350	220	330	50	170	550	-	Kimmins and Krumlik, 1976
Picea rubens - Abies balsamea (N)	all-aged	132.0	387	52	159	413	36	Weetman and Webber, 1972
Picea rubens - Abies balsamea (N)	all-aged	152.5	239	35	133	337	37	Freedman et al., 1980 a
Picea rubens - Abies fraseri (N)	50	180	-	37	177	354	72	Weaver, 1975
Picea abies(P)	20	218.3	859	99	437	357	82	Ovington, 1962
Picea abies (P)	33	43.1	204	33.9	27.2	207	10.0	Fornes et al., 1970
Picea abies (P)	47	262.7	705	82	226	507	85	Ovington, 1962

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Picea abies (P)	47	139.8	331	37	161	212	39	Ovington, 1962
Picea abies (P)	52	132.2	311	41	141	202	35	Tamm and Carbonnier, 1961
Picea abies (P)	55	311	770	87.2	427	459	69.2	Nihlgard, 1972
Picea abies (P)	58	108.6	214	31	137	259	-	Tamm and Carbonnier, 1961
Picea abies (P)	70	-	372	40.6	161	409	-	Malkonen, 1973
Picea glauca (P)	40	140.8	382	57.4	259	719	40.3	Alban et al., 1978
Picea mariana (N)	65	107.2	167	42	84	277	27	Weetman and Webber, 1972
Pinus spp. (P)	50	-	-	42.0	178	329	-	Rennie, 1955
Pinus spp. (P)	100	-	-	51.9	225	502	-	Rennie, 1955
Pinus banksiana (range)(N)	29-57	-	120-170	20-25	65-80	60	20	MacLean and Wein, 1977
Pinus banksiana (N)	30	-	153.0	12.9	74.0	99.2	15.7	Foster and Morrison, 1976
Pinus banksiana (P)	40	147.3	259	24.7	97	199	37.7	Alban et al., 1978
Pinus banksiana (N)	65	113.7	180	14	89	127	19	Morrison and Foster, 1979
Pinus contorta (N)	125	195	170	35	110	250	-	Kimmins and Krumlik, 1976
Pinus nigra (P)	18	25.8	80.7	12.0	49.3	72.9	14.6	Wright and Will, 1958
Pinus nigra (P)	28	54.3	102.0	13.7	79.6	123.3	20.6	Wright and Will, 1958
Pinus nigra (P)	45	108.5	151	19	99	147	32	Miller et al., 1980
Pinus nigra (P)	46	232.2	436	31	195	190	53	Ovington, 1962
Pinus nigra (P)	48	97.0	185.0	22.3	133.4	156.9	38.1	Wright and Will, 1958

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Pinus ponderosa (N)	60	462	1480	92	416	1760	230	Marion, 1979
Pinus radiata (P)	26	221.9	221	28	224	130	-	Orman and Will, 1960; Will, 1968.
Pinus resinosa (P)	32	61.4	174	20.1	35.1	216	19.6	Fornes et al., 1970
Pinus resinosa (P)	40	199.4	346	41.8	175	291	57.5	Alban et al., 1978
Pinus sylvestris (P)	7	-	42	5	19	14	4	Ovington, 1959
Pinus sylvestris (P)	11	-	121	11	51	58	13	Ovington, 1959
Pinus sylvestris (P)	14	-	158	18	63	76	12	Ovington, 1959
Pinus sylvestris (P)	17	-	249	28	117	85	21	Ovington, 1959
Pinus sylvestris (P)	18	54.9	151.3	16.6	115.5	69.5	22.9	Wright and Will, 1958
Pinus sylvestris (P)	20	-	309	35	143	128	27	Ovington, 1959
Pinus sylvestris (P)	23	-	280	23	118	143	28	Ovington, 1959
Pinus sylvestris (P)	28	93.1	224.2	25.0	128.9	86.3	35.8	Wright and Will, 1958
Pinus sylvestris (P)	31	-	275	29	146	203	34	Ovington, 1959
Pinus sylvestris (P)	33	149.8	265	30	170	194	39	Ovington and Madgwick, 1959 a
Pinus sylvestris (P)	35	-	337	30	182	213	49	Ovington, 1959
Pinus sylvestris (P)	47	156.6	269	25	149	163	31	Ovington, 1962
Pinus sylvestris (P)	55	-	285	25	109	188	48	Ovington, 1959
Pinus sylvestris (P)	64	118.8	205.1	22.7	99.8	201.8	34.8	Wright and will, 1958
Pinus sylvestris (P)	70	-	148	15.0	80	115	-	Malkonen, 1973
Pinus taeda (P)	11	87	242	30	145	-	-	Pope, 1979

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Pinus taeda (P)	16	-	257	31	165	187	46	Wells and Jorgensen, 1979
Pinus taeda (P)	20	-	384	27	212	204	-	Switzer and Nelson, 1973
Pinus taeda (P)	29	390	1250	78	350	1480	200	Marion, 1979
Pinus taeda (P)	40	-	568	40	344	174	-	Switzer and Nelson, 1973
Pseudotsuga menziesii (N)	15-20	64.8	185	31.0	102	196	23.2	Webber, 1977
Pseudotsuga menziesii (P)	36	171.5	288	60	196	296	-	Cole et al., 1967
Pseudotsuga menziesii (N)	36	205	320	66	220	333	50	Turner et al., 1976
Pseudotsuga menziesii (P)	47	252.4	468	49	209	338	62	Ovington, 1962
Pseudotsuga menziesii (N)	50	657	2100	131	590	2500	330	Marion, 1979
Pseudotsuga menziesii (N)	73	294	350	54	353	433	58	Turner, 1975
Pseudotsuga menziesii (N)	95	348	445	80	254	433	58	Turner, 1975
Pseudotsuga menziesii (N)	450	530	313	42	242	620	-	Abee and Lavender, 1972; Grier et al. 1974.
Tsuga heterophylla - (N) Chamaecyparis nootkatensis	⩽500	60	75	20	65	110	-	Kimmins and Krumlik, 1977
Tsuga heterophylla (N)	50	936	2995	187	842	3560	470	Marion, 1979
Tsuga mertensiana - (N) Abies amabalis	⩽550	470	560	110	410	750	-	Kimmins and Krumlik, 1977
Beans	1	3.89	120	14	62	24	7	Russell, 1973
Corn Crop	1	-	135	23	33	16	20	Foth and Turk, 1972
Corn Crop	1	-	174	28	58	23	26	Fried and Broeshart, 1967

TABLE 1 (cont.)

STAND	AGE Yr	BIOMASS MT/ha	N Kg/ha	P Kg/ha	K Kg/ha	Ca Kg/ha	Mg Kg/ha	Reference
Mangolds (+ roots)	1	8.49	167	26	280	34	29	Russell, 1973
Meadow Hay	1	3.16	55	6	48	26	10	Russell, 1973
Oats	1	4.47	59	10	43	9	6	Russell, 1973
Potatoes (+ roots)	1	3.76	52	11	71	3	4	Russell, 1973
Red Clover Hay	1	4.21	110	12	80	72	19	Russell, 1973
Turnips (+ roots)	1	5.23	123	16	139	59	6	Russell, 1973
Wheat	1	-	50	11	13	1	6	Foth and Turk, 1972
Wheat	1	4.69	56	10	27	7	5	Russell, 1973

TABLE 2. A selection of data to illustrate the effect of site variation on the standing crops of above-ground biomass and nutrients for particular tree species.

Species	Site	Age	Biomass MT/ha	N kg/ha	P kg/ha	K kg/ha	Ca kg/ha	Mg kg/ha	Reference
Platanus occidentalis	a)	3	9.2	52	10	21	46	17	Wood *et al.*, 1977
	b)	3	13.7	90	21	53	53	24	
Picea abies	a)	47	263	705	82	226	507	85	Ovington, 1962
	b)	47	140	331	37	161	212	39	

TABLE 3. A selection of data to represent the effects of species on the standing crops of above-ground biomass and nutrients in adjacent 40-year old plantations growing on a fine sandy-loam soil in Minnesota (after Alban *et al.* 1978).

Species	Age	Biomass (MT/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)
Pinus resinosa	40	199	155	42	175	291	58
Pinus banksiana	40	141	118	25	97	199	38
Picea glauca	40	141	102	57	229	719	40
Populus tremuloides - *P. grandidentata*	40	167	199	47	287	848	58

TABLE 4. Summary of literature relevant to the relative removals of biomass and nutrients by various clear-cutting treatments. C = conventional bole-only clear-cut; WT = whole-tree (above-ground) clear-cut; CT = complete-tree (above and below-ground) clear-cut; N = natural stand; P = plantation; % = percent increase of whole-tree or complete-tree removals over conventional clear-cut.

STAND	AGE		BIOMASS MT/ha	%	N kg/ha	%	P kg/ha	%	K kg/ha	%	Ca kg/ha	%	Mg kg/ha	%	Reference
Northern Hardwoods (N)	55	C	41.3		134		11.0		71		193		18.9		Whittaker et al., 1979
		WT	60.4	46	371	177	35.3	221	155	119	403	109	37.8	100	
		CT	73.2	77	552	312	88.0	700	218	208	504	161	51.3	171	
Acer rubrum-Fagus grandifolia-Betula papyrifera (N)	Mature	C	-		165		-		-		234		-		Hornbeck, 1977
		WT	-		386	134	-		-		437	87	-		
Acer rubrum -Fagus grandifolia -Betula papyrifera (N)	90	C	145		207		-		-		287		-		Hornbeck, 1977
		WT	203	40	483	133	-		-		541	89	-		
Betula lutea-Acer saccharum (N)	>80	C	128.5		42.1		3.7		24.1		73.0		5.3		Young, 1974
		WT	164.2	28	-		-		-		-		-		
		CT	238.0	85	133.0	216	18.2	392	77.1	220	181.9	149	15.2	187	
Betula papyrifera-Acer rubrum (N)	29	C	70.6		172		21.9		94		229		20.3		Ribe, 1974
		WT	79.8	13	237	38	32.1	47	128	36	283	24	29.4	45	
Fagus grandifolia-Acer saccharum-Tsuga canadensis (N)	4	C	4.5		18.9		2.0		10.1		8.4		0.5		Safford and Filip, 1974
		WT	5.4	20	34.6	83	3.0	50	15.6	54	11.9	42	1.2	140	
Populus tremuloides-Betula papyrifera (N)	45-50	C	120.3		120.3		12.1		60.2		241		24.1		Boyle and Ek, 1972
		WT	166.9	39	206.6	72	21.4	77	106.9	78	441	83	42.8	78	
Acer rubrum (N)	18	C	27.8		70.6		11.1		44.5		139		10.5		Ribe, 1974
		WT	37.2	34	164.9	134	23.6	113	86.3	94	202	45	20.6	96	
Acer rubrum (N)	30	C	49.5		125.5		19.8		79.4		248		18.6		Ribe, 1974
		WT	57.4	16	192.4	53	28.6	44	108.8	37	301	21	25.8	39	
Alnus incana (P)	22	C	83.1		220		26		50		280		16		Ovington, 1962
		WT	111.1	34	640	191	56	115	128	156	584	109	39	144	

TABLE 4 (cont.)

STAND	AGE		BIOMASS MT/ha	%	N kg/ha	%	P kg/ha	%	K kg/ha	%	Ca kg/ha	%	Mg kg/ha	%	REFERENCE
Betula papyrifera (N)	39	C	121.7		284		29.3		133		239		29.1		Ribe, 1974
		WT	131.4	8	333	17	39.7	35	168	26	278	16	39.9	37	
Betula verrucosa (P)	22	C	43.1		62		8		17		120		7		Ovington, 1962
		WT	60.8	41	240	287	30	275	62	265	312	160	24	243	
Betula verrucosa (N)	24	C	48.0		73		6		29		132		13		Ovington and
		WT	62.2	30	188	158	14	133	78	169	233	77	24	85	Madgwick, 1959b
		CT	79.1	65	277	279	19	217	93	221	312	136	28	115	
Betula verrucosa (N)	55	C	134.5		145		11		69		275		26		Ovington and
		WT	164.0	22	391	170	27	145	154	123	497	81	46	77	Madgwick, 1959b
		CT	213.8	59	543	274	34	209	200	190	651	137	60	131	
Fagus sylvatica (N)	39	C	97.9		128		16		94		79		28		Ovington, 1962
		WT	133.4	36	283	121	38	138	185	97	151	91	42	50	
Fagus sylvatica (N)	90	C	245		340		21.0		283		481		69.3		Nihlgard and
		WT	314	28	670	97	47.6	127	421	49	866	80	103.5	49	Lindren, 1977
		CT	355	45	-		-		-		-		-		
Fagus sylvatica (N)	90	C	221		290		22.4		201		201		56.6		Nihlgard and
		WT	324	47	950	228	77.6	246	429	113	582	190	97.5	72	Lindren, 1977; Nihlgard,
		CT	373	69	-		-		-		-		-		1972
Fagus sylvatica (N)	100	C	166		220		20.0		208		200		53.5		Nihlgard and
		WT	225	36	570	159	55.8	179	302	45	458	129	80.4	50	Lindren, 1977
		CT	259	56	-		-		-		-		-		
Platanus occidentalis (P)	3	C	5.9		15.4		4.7		13.7		21.5		7.8		Wood et al., 1977
		WT	9.2	56	52.3	240	9.6	104	20.8	52	45.7	113	16.7	114	
Platanus occidentalis (P)	3	C	9.1		40.0		12.5		22.0		20.5		8.3		Wood et al., 1977
		WT	13.7	51	89.7	124	21.0	68	52.5	139	52.9	158	23.9	188	
Populus deltoides (P)	1	C	0.82		2.5		0.4		2.7		3.5		0.7		Baker and
		WT	2.42	195	29.5	1080	2.5	525	20.0	640	27.5	686	5.3	657	Blackman, 1977
		CT	3.68	349	43.5	1640	7.7	1825	34.7	1185	36.5	943	6.4	814	
Populus deltoides	6-9	C	-		94		15		99		226		24		White, 1974
($\bar{x}$ of 8 stands) (P)		WT	-		209	122	29	91	177	79	348	54	37	54	

TABLE 4 (cont.)

STAND	AGE		BIOMASS MT/ha	%	N kg/ha	%	P kg/ha	%	K kg/ha	%	Ca kg/ha	%	Mg kg/ha	%	REFERENCE
Populus tremuloides-P. grandidentata (P)	40	C	147		199		26.2		198		606		39.2		
		WT	167	14	368	85	46.5	77	287	45	848	40	57.6	47	Alban et al., 1978
		CT	205	39	457	130	66.5	154	367	85	1064	76	75.6	93	
Populus tremuloides (N)	45	C	52.5		140.1		12.6		68.3		278		21.3		
		WT	58.0	10	195.0	39	18.0	43	93.7	37	327	18	28.0	30	Ribe, 1974
Quercus robur-Fraxinus excelsior (N)	115-160	C	210		396		18		219		769		58		
		WT	284	35	947	139	64	256	493	125	1338	74	126	117	Duvigneaud and Denaeyer-De Smet
		CT	336	60	1260	218	96	433	624	185	1648	114	156	169	1967
Quercus petraea (P)	21	C	28.3		70		6		41		58		11		
		WT	42.4	50	284	306	19	217	102	149	119	105	28	155	Ovington, 1962
Quercus robur (N)	47	C	106.6		218		11		118		173		23		
		WT	138.3	30	369	69	32	191	223	89	246	42	41	78	Ovington, 1962
Larix decidua (P)	46	C	145.8		108		13		32		72		21		
		WT	43.6	30	465	331	44	238	142	344	172	139	35	66	Ovington, 1962
Picea abies (P)	20	C	157.2		260		34		136		190		34		
		WT	218.3	39	859	230	99	191	437	221	357	88	82	141	Ovington, 1962
Picea abies (P)	33	C	21.7		26.7		5.8		6.4		58		3.1		
		WT	43.1	99	203.8	663	33.9	484	27.2	325	207	257	10.0	223	Fornes et al., 1970
Picea abies (P)	47	C	182.4		132		18		60		198		35		
		WT	262.7	44	705	434	82	356	226	277	507	156	85	143	Ovington, 1962
Picea abies (P)	47	C	107.9		105		11		44		107		19		
		WT	139.8	30	331	215	37	236	161	266	212	98	39	105	Ovington, 1962
Picea abies (P)	52	C	105.8		109		12		65		108		18		
		WT	132.2	25	311	185	41	242	141	117	202	87	35	94	Tamm and Carbonnier, 1961
Picea abies (P)	55	C	262		270		28.5		172		283		38.9		
		WT	311	19	770	185	87.2	206	437	154	459	62	69.2	78	Nihlgard, 1972
Picea abies (P)	58	C	85.2		63		8		52		120		-		
		WT	108.6	27	214	240	31	288	137	163	259	116	-		Tamm and Carbonnier, 1961

TABLE 4 (cont.)

STAND	AGE		BIOMASS MT/ha	%	N kg/ha	%	P kg/ha	%	K kg/ha	%	Ca kg/ha	%	Mg kg/ha	%	REFERENCE
Picea abies (P)	70	C	-		95		8.4		47		184		-		Malkonen, 1973
		WT	-		372	292	40.6	383	161	243	409	122	-		
Picea glauca-Abies lasiocarpa (N)	< 350	C	176		153		19		129		367		-		Kimmins and Krumlik, 1976
		WT	220	25	330	116	50	163	170	32	550	50	-		
Picea glauca (P)	40	C	99		102		13.2		63		246		13.6		Alban et al., 1978
		WT	141	42	382	275	57.4	335	229	263	719	192	40.3	196	
		CT	175	77	449	340	64.4	388	254	303	809	229	46.3	240	
Picea mariana (N)	65	C	53.9		43		12		25		98		8		Weetman and Webber, 1972
		WT	107.2	99	167	288	42	250	84	236	277	183	27	238	
Picea rubens-Abies balsamea (N)	80	C	163.7		31.5		4.0		21.0		57.6		6.6		Young, 1974
		WT	226.3	38	-		-		-		-		-		
		CT	310.6	90	140.2	345	26.4	560	64.1	205	181.5	215	20.1	205	
Picea rubens-Abies balsamea (N)	all-aged	C	82.3		74		11		47		150		14		Weetman and Webber, 1972
		WT	132.0	60	387	423	52	373	159	238	413	175	36	157	
Picea rubens-Abies balsamea (N)	all-aged	C	118		120		18.2		76		219		20.4		Freedman et al., 1981
		WT	153	30	239	99	35.2	93	133	74	337	54	36.9	81	
Picea rubens-Abies balsamea-Acer rubrum -Betula papyrifera (N)	mature	C	114.3		28.3		3.0		17.7		50.8		4.8		Young, 1974
		WT	155.7	36	-		-		-		-		-		
		CT	220.0	92	110.3	290	16.7	457	59.2	234	146.8	189	14.7	206	
Picea rubens-Abies balsamea (N)	mature	C	164.0		80		10		52		143		-		Norton and Young, 1976
		CT	311.1	90	346	333	65	550	158	204	448	213	-		
Pinus banksiana (N)	30	C	-		48.8		4.5		33.7		51.4		8.1		Foster and Morrison, 1976
		WT	-		153.0	214	12.9	187	74.0	120	99.2	93	15.7	94	
Pinus banksiana (P)	40	C	118		118		9.3		52		128		22.2		Alban et al., 1978
		WT	147	25	259	119	24.7	166	97	87	199	55	37.7	70	
		CT	175	48	296	151	29.7	219	119	129	241	88	45.7	106	
Pinus banksiana (N)	65	C	90.1		82		4		50		87		12		Morrison and Foster, 1979
		WT	113.7	26	180	120	14	250	89	78	127	46	19	58	
		CT	136.9	52	204	149	17	325	105	110	155	78	25	108	

TABLE 4 (cont.)

STAND	AGE		BIOMASS		N		P		K		Ca		Mg		REFERENCE
			MT/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	
Pinus contorta (N)	125	C	170		110		23		96		217		-		Kimmins and Krumlik, 1976
		WT	195	15	170	55	35	52	110	15	250	15	-		
Pinus nigra (P)	18	C	16.3		27.5		3.6		14.6		25.8		6.1		Wright and Will, 1958
		WT	25.8	58	80.7	193	12.0	233	49.3	238	72.9	183	14.6	139	
Pinus nigra (P)	28	C	52.7		46.0		5.4		34.2		49.3		9.5		Wright and Will, 1958
		WT	54.3	3	102.0	122	13.7	154	79.6	133	123.3	150	20.6	117	
Pinus nigra (P)	45	C	102		74		7.7		45		82		18.5		Miller et al., 1980
		WT	109	7	151	104	18.9	145	99	120	147	79	31.5	70	
Pinus nigra (P)	46	C	212.0		207		14		102		115		39		Ovington, 1962
		WT	242.2	14	436	111	31	121	195	91	190	65	53	36	
Pinus nigra (P)	48	C	95.3		98.1		10.8		68.4		79.6		21.7		Wright and Will, 1958
		WT	97.0	2	185.0	89	22.3	106	133.4	95	156.9	97	38.1	76	
Pinus radiata (P)	26	C	201.8		128		18		158		105		-		Orman and Will, 1960; Will, 1968
		WT	222.0	10	221	73	28	56	224	42	130	24	-		
		CT	250.0	24	255	99	41	128	252	59	158	50	-		
Pinus resinosa (P)	32	C	40.5		53.7		6.8		12.3		107		7.4		Fornes et al., 1970
		WT	61.4	52	173.6	223	20.1	196	35.1	185	216	102	19.6	165	
Pinus resinosa (P)	40	C	160		155		15.3		84		185		34.2		Alban et al., 1978
		WT	199	24	346	123	41.8	173	175	108	291	57	57.9	69	
		CT	243	52	421	172	49.8	225	205	144	335	81	71.9	110	
Pinus sylvestris (P)	7	C	-		4		1		3		2		1		Ovington, 1959
		WT	-		42	950	5	400	19	663	14	600	4	300	
		CT	-		69	1625	9	800	26	767	18	800	6	500	
Pinus sylvestris (P)	11	C	-		11		1		8		7		2		Ovington, 1959
		WT	-		121	1000	11	1000	51	663	58	729	13	550	
		CT	-		182	1555	18	1700	66	725	69	886	18	800	
Pinus sylvestris (P)	14	C	-		17		2		10		12		2		Ovington, 1959
		WT	-		158	829	18	800	63	530	76	533	12	500	
		CT	-		219	1188	29	1350	76	660	86	617	17	750	

TABLE 4 (cont.)

STAND	AGE		BIOMASS MT/ha	%	N kg/ha	%	P kg/ha	%	K kg/ha	%	Ca kg/ha	%	Mg kg/ha	%	REFERENCE
Pinus sylvestris (C)	17	C	-		33		4		19		19		4		Ovington, 1959
		WT	-		249	655	28	600	117	516	85	347	21	425	
		CT	-		311	842	38	850	138	632	99	421	27	575	
Pinus sylvestris (P)	18	C	35.6		52.7		5.4		42.6		30.3		10.3		Wright and Will, 1958
		WT	54.9	54	151.3	187	16.6	207	115.5	171	69.5	129	22.9	122	
Pinus sylvestris (P)	20	C	-		48		6		29		31		7		Ovington, 1959
		WT	-		309	544	35	483	143	393	128	313	27	286	
		CT	-		397	727	46	666	170	486	144	365	35	400	
Pinus sylvestris (P)	23	C	-		59		5		34		56		8		Ovington, 1959
		WT	-		280	375	23	360	118	247	143	155	28	250	
		CT	-		469	695	34	580	153	350	191	241	44	450	
Pinus sylvestris (P)	28	C	75.4		96.4		10.1		65.6		47.1		22.6		Wright and Will 1958
		WT	94.1	25	224.2	133	25.0	148	128.9	96	86.3	83	35.8	58	
Pinus sylvestris (P)	31	C	-		73		8		49		104		13		Ovington, 1959
		WT	-		275	277	29	263	146	198	203	95	34	162	
		CT	-		384	426	47	488	199	306	334	221	51	292	
Pinus sylvestris (P)	33	C	118.8		97		12		84		115		24		Ovington and Madgwick, 1959a
		WT	149.8	26	265	173	30	150	170	102	194	69	39	63	
		CT	185.9	56	346	257	41	242	224	167	227	97	52	117	
Pinus sylvestris (P)	35	C	-		86		7		64		124		28		Ovington, 1959
		WT	-		337	292	30	329	182	184	213	72	49	75	
		CT	-		501	483	63	800	243	280	364	194	72	157	
Pinus sylvestris (P)	47	C	129.6		90		8		54		119		25		Ovington, 1962
		WT	156.6	21	269	199	25	213	149	176	163	37	31	24	
Pinus sylvestris (P)	55	C	-		88		7		46		122		28		Ovington, 1959
		WT	-		285	224	25	257	109	137	188	54	48	71	
		CT	-		469	433	42	500	152	230	281	130	68	143	
Pinus sylvestris (P)	64	C	97.4		100.9		10.6		51.6		143.5		23.0		Wright and Will, 1958
		WT	118.8	22	205.1	103	22.7	114	99.8	93	201.8	41	44.8	95	

TABLE 4 (cont.)

STAND	AGE		BIOMASS MT/ha	%	N kg/ha	%	P kg/ha	%	K kg/ha	%	Ca kg/ha	%	Mg kg/ha	%	REFERENCE
Pinus sylvestris (P)	70	C	-		58		5.3		38		73		-		Malkonen, 1973
		WT	-		148	155	15.0	183	80	111	115	58	-		
Pinus taeda (P)	20	C	-		292		17		168		178		-		Switzer and Nelson, 1973
		WT	-		384	32	27	59	212	26	204	15	-		
Pinus taeda (P)	40	C	-		464		28		292		152		-		Switzer and Nelson, 1973
		WT	-		568	22	40	43	344	18	174	14	-		
Pinus taeda (P)	11	C	63		78		11.5		74		-		-		Pope, 1979
		WT	87	38	242	210	30.0	161	145	96	-		-		
Pseudotsuga menziesii (N)	15-20	C	42.9		67.5		7.8		28.0		49		6.8		Webber, 1977
		WT	64.8	51	185.3	175	31.0	297	102.3	265	196	300	23.2	241	
Pseudosuga menziesii (P)	36	C	140.4		125		19		96		117		-		Cole et al., 1967
		WT	171.5	22	288	130	60	216	196	104	296	153	-		
		CT	204.5	46	320	156	66	247	220	129	333	185	-		
Pseudotsuga menziesii (P)	47	C	202.7		157		15		73		92		24		Ovington, 1962
		WT	252.4	25	468	198	49	227	209	186	338	267	62	158	
Tsuga mertensiana-Abies amabalis (N)	≤550	C	392		301		66		277		507		-		Kimmins and Krumlik, 1976
		WT	470	20	560	86	110	67	410	48	750	48	-		
Tsuga heterophylla-Chamaecyparis nootkatensis (N)	≤500	C	42		28		9		37		56		-		Kimmins and Krumlik, 1976
		WT	60	43	75	168	20	122	65	76	110	96	-		

TABLE 5. Summary of a sampling of the literature relevant to the content of nutrients in the forest floor or mineral soils of a variety of forest types. T = total amounts of nutrients; A = available or exchangeable amounts of nutrients; ff = forest floor; ms = mineral soil.

Forest	Location	Horizon and Depth		N ($kgha^{-1}$)	P ($kgha^{-1}$)	K ($kgha^{-1}$)	Ca ($kgha^{-1}$)	Mg ($kgha^{-1}$)	Reference
Northern hardwoods	Hubbard Brook, N.H.	ff	T	1,260	80	70	370	40	Likens et al., 1977
		ms (exploitable)	T	-	-	-	9,600	-	
		ms	A	-	-	-	510	-	
Mixed hardwoods	Wisconsin	surface soil	T	1,800	-	-	-	-	Boyle and Ek, 1972
		(2 cm)	A	-	180	190	760	210	
Northern hardwoods	New Hampshire	exploitable soil	T	10,400	2,100	-	13,300	-	Hornbeck and Kropelin, 1979
Acer saccharum	Nova Scotia	ff (6 cm)	T	760	45	70	250	24	Freedman et al, 1980
			A	4	2	10	54	6	
		ms (50 cm)	T	7,200	3,400	14,600	20,700	3,300	
			A	69	160	83	657	56	
Acer saccharum - Betula papyrifera	Nova Scotia	ff (6 cm)	T	1,040	84	147	113	20	Freedman et al, 1980
			A	4	3	11	28	5	
		ms (47 cm)	T	12,500	3,320	24,200	13,400	9,100	
			A	20	245	130	262	49	
Acer saccharum - A. rubrum Betula allegheniensis	Nova Scotia	ff (4 cm)	T	450	23	43	87	8	Freedman et al., 1980
			A	2	1	3	16	2	
		ms (37cm)	T	8,280	1,220	22,200	11,400	1,700	
			A	42	27		235	51	
Alnus rubra	Washington	ff	T	360	27	42	150	13	Turner et al., 1976
		ms (60 cm)	T	5,450	3,920	77,200	106,600	110,700	
		ms (60 cm)	A	-	140	150	840	120	

TABLE 5 (cont.)

Forest	Location	Horizon and Depth		N kgha^{-1}	P kgha^{-1}	K kgha^{-1}	Ca kgha^{-1}	Mg kgha^{-1}	Reference
Betula papyrifera - *Acer rubrum*	Nova Scotia	ff (6 cm)	T	850	53	110	350	40	Freedman *et al.*, 1980
			A	4	2	2	12	2	
		ms (44 cm)	T	5,300	1,900	12,700	16,600	4,200	
			A	68	193	20	79	14	
Populus grandidentata - *P. tremuloides*	Nova Scotia	ff (2 cm)	T	75	10	40	50	5	Freedman *et al.*, 1980
			A	1	1	2	11	2	
		ms (50 cm)	T	5,900	2,900	23,000	17,000	7,700	
			A	96	284	154	248	44	
Populus tremuloides	Minnesota	ff	T	67	-	-	-	-	Alban *et al.*, 1978
			A	-	60	80	1,090	90	
		ms (36 cm)	T	2,060	-	-	-	-	
			A	-	90	290	2,640	270	
Populus tremuloides	Wisconsin	exploitable soil (15 cm)	A	24	100	120	590	-	Boyle *et al.*, 1973
Quercus - *Carya*	North Carolina	ff	T	140	-	20	130	-	Henderson *et al.*, 1978
		ms (60 cm)	T	6,800	-	124,000	2,500		
		ms	A	120	-	510	940	-	
Quercus-Carya	Tennessee	ff	T	310	-	20	430	-	Henderson *et al.*, 1978
		ms (60 cm)	T	4,700	-	38,000	3,800		
		ms	A	80		170	710		
Boreal Forest (typical)	-	ff	T	700	-	-	-	-	Krause *et al.*, 1979
			A	-	80	270	160	-	
		ms	T	1,560	-	-	-	-	
			A	-	200	110	90	-	
Upland Boreal Forest (typical)	-	soil to rooting depth	T	2,000	400	20,000	4,000	4,000	Weetman and Webber, 1972
			A	20	35	200	500	100	

TABLE 5 (cont.)

Forest	Location	Horizon and Depth		N kg ha^{-1}	P kgha^{-1}	K kgha^{-1}	Ca kgha^{-1}	Mg kgha^{-1}	Reference
Picea glauca	Minnesota	ff	T	750	-	-	-	-	Alban et al., 1978
			A	-	60	80	1,400	80	
		ms (36 cm)	T	2,540	-	-	-	-	
			A	-	70	300	2,810	340	
Picea glauca	Nova Scotia	ff (4 cm)	T	590	40	53	110	10	Freedman et al., 1980
			A	2	1	6	14	2	
		ms (45 cm)	T	5,700	1,280	14,100	19,400	3,780	
			A	49	64	97	234	30	
Picea mariana	Quebec	exploitable	T	1,150	680	17,200	2,320	3,040	Weetman and Webber, 1972
		soil (35 cm)	A	31	30	130	45	48	
Picea mariana	Nova Scotia	ff (7 cm)	T	690	50	130	110	30	Freedman et al., 1980
			A	4	2	11	20	7	
		ms (27 cm)	T	4,180	950	10,900	3,500	460	
			A	59	61	71	89	28	
Picea rubens - Abies balsamea	Quebec	exploitable	T	2,020	210	10,400	1,270	1,020	Weetman and Webber, 1972
		soil (26 cm)	A	14	6	65	29	120	
Picea rubens - Abies balsamea	Nova Scotia	ff (10 cm)	T	1,030	75	150	210	60	Freedman et al., 1980
			A	4	4	15	35	9	
		ms (28 cm)	T	2,830	630	12,000	4,900	1,020	
			A	38	96	63	117	29	
Picea rubens - Abies balsamea	Nova Scotia	ff (8 cm)	T	900	62	110	290	32	Freedman et al., 1981
			A	2	3	12	33	9	
		ms (31 cm)	T	3,860	1,220	13,300	5,460	1,740	
			A	45	102	61	77	30	

TABLE 5 (cont.)

Forest	Location	Horizon and Depth		N gha^{-1}	P gha^{-1}	K gha^{-1}	Ca gha^{-1}	Mg gha^{-1}	Reference
Pinus banksiana	Minnesota	ff	T	690	-	-	-	-	Alban *et al*, 1978
			A	-	50	70	778	80	
		ms (36 cm)	T	2,310	-	-	-	-	
			A	-	70	280	3,800	320	
Pinus banksiana	Northern Ontario	ff	A	14	2	37	100	12	Foster and Morrison, 1976
		ms (100 cm)		15	29	390	190	29	
Pinus resinosa	Minnesota	ff	T	540	-	-	-	-	Alban *et al.*, 1978
		ms (36 cm)	A	-	40	60	660	70	
		ms (36 cm)	T	2,750	-	-	-	-	
			A	-	80	300	3,900	330	
Pseudotsuga menziesii - *Tsuga heterophylla*	Oregon	ff	T	740	-	90	570	-	Henderson *et al.*, 1978
		ms (60 cm)	T	4,500	-	-	-	-	
		ms (60 cm)	A	5	-	860	4,450	-	
Picea glauca - *Abies amabalis*	British Columbia	ff	T	850	100	100	300	-	Kimmins, 1977
		ms (rooting depth)	T	3,500	4,700	4,500	3,800	-	
		ms (100 cm)	A	50	400	400	1,200	-	

TABLE 6. Summary of a sampling of the literature relevant to precipitation inputs of nutrients to watersheds or forests.

Location	N Kg ha^{-1} yr^{-1}	P Kg ha^{-1} yr^{-1}	K Kg ha^{-1} yr^{-1}	Ca Kg ha^{-1} yr^{-1}	Mg Kg ha^{-1} yr^{-1}	Reference
Maine	1.9 - 2.5	2.9	2.9	13.0	-	Pearson and Fisher, 1971
Massachusetts	2.2 - 2.3	-	2.0 - 5.6	2.4 - 4.9	-	Pearson and Fisher, 1971
New York State	7.9 - 9.4	-	3.6 - 3.9	9.9 - 23.5	-	Pearson and Fisher, 1971
Connecticut	2.5	-	1.6	4.9	-	Pearson and Fisher, 1971
Ithaca, New York	9.8	0.07	0.8	14.9	1.5	Likens, 1972
Aurora, New York	11.5	0.12	1.1	14.7	2.2	Likens, 1972
Geneva, New York	7.0	0.05	0.4	3.4	0.6	Likens, 1972
Canoga, New York	5.2	0.38	1.2	5.4	0.8	Likens, 1972
Lodi, New York	8.0	0.22	1.5	4.0	0.6	Likens, 1972
Watkins Glen, New York	10.6	0.21	1.5	15.4	3.2	Likens, 1972
Hubbard Brook, N.H. (wet only)	5.8	0.04	0.9	2.2	0.6	Likens et al., 1977; Whittaker et al., 1979
Kejimkujik, Nova Scotia	11.9	-	0.9	7.3	5.4	Kerekes, 1980
Nathwaak, New Brunswick	2.7	0.1	1.0	2.2	0.4	Powell, 1978
Clear Lake, Southern Ontario	10.0	0.35	1.0	14.1	5.4	Schindler and Nightswander, 1970
Rawson Lake, Northwestern Ontario	6.3	0.33	1.1	3.8	0.9	Schindler et al., 1976
Coweeta, North Carolina	4.9	0.19	0.4	4.7	1.5	Swank, 1976; Henderson et al., 1977a, 1978

TABLE 6 (cont.)

Location	N Kg ha^{-1} yr^{-1}	P Kg ha^{-1} yr^{-1}	K Kg ha^{-1} yr^{-1}	Ca Kg ha^{-1} yr^{-1}	Mg Kg ha^{-1} yr^{-1}	Reference
Walker Branch, Tennessee	5.9	0.54	3.1	14.3	2.1	Henderson et al., 1977a, 1978
Utah	12.0	1.5	4.5	3.7	3.1	Stark, 1979
Oregon	1.1	0.0	0.8	2.8	-	Cole et al., 1967
Eugene, Oregon	0.7	-	0.4	4.7	0.4	Henderson et al., 1978
Northwestern United States	1.3	0.2	0.1	2.1	1.3	Abee and Lavender, 1972
Southwestern British Columbia	3.7	0.0	0.9	3.6	0.9	Feller and Kimmins, 1979
Jamieson Creek, B.C.	1.7	0.4	0.8	7.3	2.2	Zeman 1973, 1975
Carnation Creek, Vancouver Island.	2.7	0.11	2.5	3.7	3.0	Scrivener, 1975
Finland (average)	5.9	0.09	2.5	2.0	1.3	Viro, 1953
Solling, C. Germany	23.7	0.7	3.8	13.9	2.2	Heinrichs and Mayer, 1977; Mayer and Ulrich, 1977

TABLE 7. Typical inputs of nutrients with incident precipitation, as calculated from the data of Table 6. All data are in units of kg ha^{-1} yr^{-1}.

	N	P	K	Ca	Mg
$\bar{x} \pm$ S.D.	6.2 ±5.0	0.4 ± 0.7	1.7 ±1.3	7.2 ±5.3	1.7 ±1.3
Range	0.7 - 23.7	0.0 - 1.5	0.1 - 5.6	2.0 - 23.5	0.4 - 5.4
Number of Sites	25	21	25	25	20

TABLE 8. Summary of literature relevant to rates of primary weathering in a variety of forested watersheds.

Forest	Bedrock	Location	N Kg ha^{-1} yr^{-1}	P Kg ha^{-1} yr^{-1}	K Kg ha^{-1} yr^{-1}	Ca Kg ha^{-1} yr^{-1}	Mg Kg ha^{-1} yr^{-1}	Reference
Northern hardwoods	moraine/gneiss	Hubbard Brook, N.H.	0	?	7.1	21.1	3.5	Johnson et al., 1968; Clayton, 1979; Whittaker et al., 1979.
Mixed hardwoods	outwash sands	Long Is., N.Y.	-	-	11.1	24.2	8.4	Woodwell and Whittaker 1967; Clayton, 1979
Mixed hardwoods	schists	Maryland	-	-	2.3	1.3	1.1	Cleaves et al., 1970
Coastal hardwoods	quartz sands	New York	-	-	0.01	0.04	0.01	Art et al., 1974
Populus tremuloides - mixed hardwoods	glacial hill	Wisconsin	-	0.9	3.6	7.1	-	Boyle et al., 1973
Pseudotsuga-Tsuga -Thuja	various, 80% plutonic	s.w. B.C.	~0	0.33	1.7	34.4	6.6	Zeman, 1975
range of 8 studies	various		-	-	tr-11	tr-86	2-52	Clayton, 1979

TABLE 9. Rates of nitrogen fixation in a variety of forest stands.

Stand	Location	Site of Fixation	Rate of N_2 Fixation ($kg\ ha^{-1}\ yr^{-1}$)	Reference
Acer rubrum	Nova Scotia	aboreal lichen only	0.0035	Blacklock *et al.*, 1980
Quercus -*Carya*	North Carolina	arboreal lichens only	0.0012	Becker *et al.*, 1977
Pseudotsuga menziesii	nw U.S.	free-living (phyllosphere)	7-23	Burns and Hardy, 1975
northern hardwoods	New Hampshire	free living (decaying wood)	11-17	Bormann *et al.*, 1977; Likens *et al.*, 1977, 1978
northern hardwoods(20-40 yr)	ne U.S.	free living (decaying wood)	~ 28	Bormann and Likens, 1979
northern hardwoods(140-170 yr)	ne U.S.	free living (decaying wood)	~ 2	Bormann and Likens, 1979
montane	Montana	free-living (decaying wood)	0.89	Larsen *et al.*, 1978
Pseudotsuga menziesii	Britain	various free-living	7.6 - 19.7	Jones *et al.*, 1974
Quercus - *Carya*	se U.S.	various free-living	12.0	Todd *et al.*, 1978
Alnus spp.	various studies reviewed	root nodule symbionts	12-300 (range)	Tarrant and Trappe, 1971
Alnus rubra	nw U.S.	root nodule symbionts	320	Wollum and Davey, 1975
Ceonothus velutinus	nw U.S.	root nodule symbionts	> 100	Wollum and Davey, 1975

TABLE 10. Summary of literature relevant to net fluxes of nutrients (i.e. total inputs minus total outputs) for a variety of undisturbed watersheds. W = watershed study; L = lysimeter study; all data in kg ha^{-1} yr^{-1}.

Forest Type	Location	Predominant Bedrock	N	P	K	Ca	Mg	Reference
Fagus sylvatica (L)	cent. Germany	loess over sandstone	+22	+0.7	+5.4	+10	+1.1	Heinrichs and Mayer, 1977; Ulrich and Mayer, 1977
Quercus-Carya (W)	Tennessee	dolomite	+1.8	+0.5	-3.7	-133	-75	Henderson et al., 1977b, 1978
Quercus-Carya-Acer (W)	North Carolina	granitics	+4.7	-	-5.2	-3	-2	Swank and Douglas, 1975; Henderson et al., 1978.
Quercus-Carya (W)	North Carolina	granitics	-	-	+0.5	-1.5	-1.7	Johnson and Swank, 1973; Best and Monk, 1975; Cromack and Monk, 1975
Acer-Fagus-Betula (W)	New Hampshire	gneissic	+16.7	+0.017	-1.5	-11.7	-2.7	Likens et al., 1967, 1977
Acer-Fagus-Quercus (W)	s. Ontario	gneissic and granitic	+ 8.7	+0.26	+0.14	+ 7.4	+3.1	Schindler and Nightswander, 1970
Mixed forest (W)	New Brunswick	granitics	-0.2	+0.2	-1.7	-32	-5.5	Powell, 1978
Acer-Fagus-Betula (W)	Nova Scotia	granitics	+23.5	-	-0.4	-9.7	-5.9	Kerekes, 1980
Mixed forest (W)	n.e. Minnesota	granitics	-	+1.2	+0.2	-0.2	-0.8	Wright, 1976
mainly Picea abies (W)	Finland	gneissic and granitic	+4	-0.17	-2.1	-10	-3	Viro, 1953
mainly Picea abies (W)	S. Norway	granitics	+11.9	-	+2.1	-6.3	-1.1	Gjessing et al., 1976
Picea abies (L)	c. Germany	loess over sandstone	+14	+0.8	+6.2	+20	+2.4	Heinrichs and Mayer, 1977
Pinus strobus (W)	North Carolina	granitics	-	-	+2.1	+1.2	-0.6	Johnson and Swank, 1973;Best and Monk, 1975; Cromack and Monk, 1975
Picea-Pinus (W)	nw Ontario	gneissics	+ 5.3	+0.28	-0.14	-2.2	-1.5	Schindler et al, 1976

TABLE 10 (cont.)

Forest Type	Location	Predominant Bedrock	N	P	K	Ca	Mg	Reference
Pseudotsuga-Tsuga (W)	Oregon	volcanics	+0.5	-	-1.3	-47	-2	Frederikson, 1972; Henderson et al, 1978
Tsuga-Thuja-Pseudotsuga (W)	sw B.C.	igneous quartzitics	+2.6	0.0	-1.2	-16	-3.3	Feller and Kimmins, 1979
Tsuga-Abies (W)	Vancouver Is.	various	+1.7	+ 0.06	-2.3	-54	-7.5	Scrivener, 1975
Pseudotsuga-Tsuga-Thuja-Abies (W)	sw B.C.	various	+0.3	- 0.33	-1.7	-34	-6.6	Zeman, 1975

TABLE 11. Summary of literature relevant to losses of nutrients to the atmosphere as a result of burning.

Community	Location	Burn	Nutrient Loss	Reference
montane coniferous	n.c. Washington	wildfire	losses via volatalization and convection were 855 kg/ha N, 282 K, 75 Ca, and 33 Mg	Grier, 1975
montane coniferous	s.w. Canada	wildfire	losses via voltalization and convection were 580 kg ha^{-1} N, 14 K, 43 Ca	Kimmins and Feller, 1976
coniferous	n.w. Europe	wildfire	atmospheric losses of 10% of total site N, ca. 320 kg/ha	Viro, 1974
pine	w. Washington	wildfire	atmospheric losses of 67% of duff N by severe fire	Isaac and Hopkins, 1937. Cited in DeBell and Ralston, 1970
mixed forest	Tasmania	slash burn	total atmospheric losses of 10 kg/ha P, 57 K, 100 Ca, and 37 Mg, representing 18% of P in fuel consumed, 17% K, 12% Ca, 29% Mg.	Harwood and Jackson, 1975.
"typical " U.S. forest	U.S.	calculated for slash burns	calculated volatalization losses for "average" slash burn of 22 kg NO_x /ha. Assumes emission factor of 1.2 kg NO_x /MT fuel consumed.	Sandburg et al., 1979
Calluna vulgaris	England	simulated	at burn of 310-580°C, had losses of 43% of N,18%S, 5%P, 7%K, 8% Ca, 4% Mg. At 590-750°C, had losses of 57% of N, 36% S, 14%P, 20% K, 12% Ca, 14% Mg.	Evans and Allen, 1971.
pine	-	simulated	lost 33% of duff N, equivalent to 72 kg N/ha	Lewis, 1975
chaparral	sw U.S.	simulated	lost 67% of total N by intense burn of dry soil,<25% when soil and litter were moist	DeBano et al., 1979; Dunn et al. 1979.
pine	nw U.S.	simulated	lost 62% of litter and leaf N by volatalization	DeBell and Ralston, 1970
Tsuga-Pseudotsuga	nw U.S.	simulated	at 300°C, lost 25% of total fuel N, or 167 kgN/ha at 700°C, lost 64% of total fuel N, or 411 kg n/ha	Knight, 1966
pine	-	simulated	volatile losses of 25% of total N in forest floor fuel	Hosking, 1938

TABLE 12. Summary of the literature relevant to the effects of fire on losses of nutrients from watersheds.

Forest	Location	Post-fire Watershed Effects	Reference
Populus tremuloides	s. Ontario	after prescribed fire, most nutrients were retained within surface soils. Soils organic with high CEC.	Smith and James, 1978.
mixed forest	ne Minnesota	wildfire increased first-year streamwater losses of P from 0.015 kg ha^{-1} yr^{-1} to 0.1, K from 0.16 to 1.4, Ca from 3.0 to 12.2, and Mg from 1.3 to 3.6	Wright, 1976
Picea-Pinus	nw Ontario	two naturally-burned watersheds. Total N losses from watersheds were ($\bar{x}$) 2.6 kg ha^{-1} yr^{-1}, c.f. 0.9 for unburned watershed. Total P losses were 0.15, c.f. 0.02. Dissolved K losses were 3.7, c.f. 0.7.	Schindler *et al.*, 1980
Pinus banksiana	n. Ontario	accelerated leaching of K, Ca for 3 post-fire months. Leaching of P apparently reduced extractable PO_4 in surface soils.	Smith, 1970
Pinus ponderosa	nw U.S.	low available N and P in soils of 12 year old burn believed due to accelerated post-fire leaching.	Wagle and Kitchen, 1972.
Pseudotsuga menziesii	Oregon	watershed clear-cut and slash burned. Streamwater NO_3-N losses in first year were 15.7 kg ha^{-1} yr^{-1}, up from pre-impact of 4.9. Returned to baseline after six years. K losses were elevated for six months. No effect on P losses.	Brown *et al.*, 1973
Pinus ponderosa - *Pseudotsuga menziesii*	e. Washington	four post-fire years of streamwater losses of N, P, K, Ca, and Mg were equivalent to 0.5, 0.01, 4, 17, and 13% of site nutrient "capital" for these nutrients. Maximum streamwater NO_3 concentration rose from <0.016 to 0.56 ppm after fire, while P, K, Ca, and Mg rose by ca 50%	Tiedemann et al., 1978
coniferous	nc Washington	few effects of wildfire on nutrient losses from montane watershed	Grier, 1975

TABLE 13. A partial list of recent studies which have examined the effects of forest harvesting on sediment or soluble nutrient losses.

Studies Documenting Increased Erosion	Studies Documenting Increased Leaching	Studies Showing No, or Minimal Effects
DeByle and Packer, 1972	Gessel and Cole, 1965	Verry, 1972
Megahan, 1972	Bormann et al., 1968, 1969, 1974	Aubertin and Patric, 1974
Rice et al., 1972	Likens et al., 1969, 1970, 1977, 1978	Richardson and Lund, 1975
Patric, 1976	DeByle and Packer, 1972	Hetherington, 1976
Corbett et al., 1978	Pierce et al., 1972	Czapowskyj et al., 1977
Hornbeck and Ursic, 1979	Brown et al., 1973	Sopper, 1975
McColl and Grigall, 1979	Dillon and Kirchner, 1975	McColl, 1978
Rice et al., 1979	Hart and DeByle, 1975	Stark, 1980b
	Hornbeck et al., 1975	
	Aber et al., 1978, 1979	
	Huff et al., 1978	
	Burger and Pritchett, 1979	
	Hornbeck and Ursic, 1979	
	Jurgensen et al., 1979b	
	Martin and Pierce, 1979	
	McColl and Grigall, 1979	
	Vitousek et al., 1979	

TABLE 14. Summary of the literature relevant to the effects of forest harvest on sediment losses from watersheds.

Forest	Location	Slope	Effects on Sediment Discharge	Reference
various forests (review)			broad estimate of soil losses by surface erosion from clear-cuts of ca. 1-5 MT ha-1 yr^{-1}. Losses can be greatly reduced by taking proper precautions during operations.	McColl and Grigall, 1979
Pinus ponderosa	Idaho	35-55%	five years of post-harvest sediment losses averaged 0.12 MT ha^{-1} yr^{-1}, compared with zero for a control watershed.	Haupt and Kidd, 1965
Pinus ponderosa	Idaho	70%	six years of post-harvest sediment losses averaged 4.0 MT ha^{-1} yr^{-1}, compared with 0.09 from a control watershed.	Megahan and Kidd, 1972
Larix occidentalis - Pseudotsuga menziesii - Picea engelmanii	Montana	24%	watershed clearcut, then slash burned. Sediment losses essentially zero on control watershed, increasing to 50, 150, 13, 15, and 0 kg ha^{-1} yr^{-1} in years 1, 2, 3, 4, and 7 after logging. Losses of nutrients with sediments (sum of first 4 years) were 1.7 kg ha^{-1} of N, 0.7P, 1.5K, 9.4 Ca, and 2.9 Mg.	Packer and Williams, 1976; DeByle and Packer, 1972
Pseudotsuga menziesii	Oregon	55%	two years of post-harvest sediment losses averaged 0.56 MT ha^{-1} yr^{-1}, compared with 0.26 from control watershed	Fredrikson, 1970
Pseudotsuga menziesii	Oregon	30-40%	sediment losses of 0.94 MT ha^{-1} yr^{-1} in first year following clear-cut, compared with 0.42 for uncut watershed.	Brown and Krygier, 1971

TABLE 15. Summary of the literature relevant to the effects of forest harvest on nutrient losses in solution from watersheds.

Forest	Location	Post-cutting Watershed Effects	Reference
northern hardwoods	New Hampshire	streamwater nutrient losses from experimentally deforested Hubbard Brook watershed were 499 Kg ha^{-1} 10 yr^{-1} of NO_3-N, 450 of Ca, and 166 of K, compared with 43 of NO_3-N, 131 of Ca and 22 of K from uncut watershed.	Bormann et al., 1968 1974; Pierce et al., 1972; Likens et al., 1978
northern hardwoods	New Hampshire	streamflow losses from commercial clear-cut watershed were 95 kg ha^{-1} of N, and 89 of Ca in first two years after harvest, compared with 144 kg ha^{-1} of N and 221 of Ca removed with wood.	Pierce et al., 1972; Likens et al., 1978
northern hardwoods	New Hampshire	streamwater losses from experimental strip-cuts were 93 kg ha^{-1} of NO_3-N, and 44 of Ca in first two years of harvest, compared with 40 kg ha^{-1} of NO_3-N and 34 of Ca from uncut watershed.	Hornbeck et al., 1975
northern hardwoods	New Hampshire	clear-cut watershed had elevated NO_3-N and Ca losses, lasting for five years before pre-cut levels were again reached. Buffer strips along streams reduced losses by ca. 50%	Martin and Pierce, 1979
northern hardwoods	s. Ontario	mean annual PO_4-P losses from forested watersheds on igneous bedrock were 0.04 kg ha^{-1} yr^{-1}, compared with 0.12 from watersheds of pasture plus forest. On sedimentary bedrock, forested watersheds averaged 0.11 kg ha^{-1} yr^{-1}, compared with 0.29 from forest plus pasture watersheds.	Dillon and Kirchner, 1975
Quercus-Acer -Liriodendron	W. Virginia	few negative effects of clear-cutting or water quality. Ascribed to careful road construction, buffer strips along streams, rapid vegetation regrowth.	Aubertin and Patric, 1974.

Forest	Location	Post-cutting Watershed Effects	Reference
hardwoods	North Carolina	mean annual nutrient concentrations in streamwater draining hardwood coppice regrowth were 120 ppb NO_3-N, 4 NH_4-N, 1 PO_4-P, 406K, and 792 Ca, compared with concentrations from undisturbed stand of 4 ppb NO_3-N, 4 NH_4-N, 1 PO_4-P, 369K, and 549 Ca.	Huff *et al.*, 1978
Populus tremuloides	Michigan	experimental 0.5 ha clear-cuts. Lysimeter collections showed no increase in concentration of N, P, K, or Mg, and only minor effect on Ca, compared with uncut forest.	Richardson and Lund, 1975
Populus tremuloides	Minnesota	streamwater concentrations draining clear-cut watershed were 0.55 ppm NH_4-N and 0.16 ppm NO_3-N, compared with 0.41 and 0.12 ppm for control, uncut watershed. Changes for other nutrients were minor. However, a flow increment of 31% from the clearcut indicates a proportional nutrient loss, even though concentrations were little affected.	Verry, 1972
Eucalyptus globulus	California	lysimeter solution concentrations of NO_3, K, Ca, and Mg were lower or clearcut than on uncut stand. Believed due to high CEC of clay soils, limited amount and duration of rainfall, and removal of slash and litter from clear-cut.	McColl, 1978
Pseudotsuga menziesii - *Alnus rubra*	Oregon	minor short-term effects of clear-cutting losses of NO_3-N and K, but overall small losses of NO_3-N, K, or Ca, relative to site capital.	Brown *et al*, 1973

Forest	Location	Post-cutting Watershed Effects	Reference
Pseudotsuga menziesii	Washington	experimental 0.08 ha clearcuts in 35-yr old plantation. Lysimeter measurements at 1 m soil depth showed losses of 1.1, 1.1 and 9.2 kg ha^{-1} yr^{-1} of N, K, and Ca, compared with control values of 0.6, 1.0, and 4.5.	Gessel and Cole, 1965
Picea-Abies-Pinus	British Columbia	no effect of clear-cutting of 25% of watershed on streamwater losses of N, P, Mg in second post-cutting year. Minor increases for K and Ca.	Hetherington 1976
Pinus elliottii - *P. palustris*	Florida	conventional clear-cut followed by slash burn and scarification by blading. Lysimeter solution concentrations were 0.16 ppm NH_4-N, 0.13 NO_3-N, 0.68 PO_4-P, and 2.83 K, compared with control values of 0.08 NH_4-N, 0.09 NO_3-N, 0.05 PO_4-P, and 0.57 K.	Burger and Pritchett, 1979
Pseudotsuga menziesii- *Pinus ponderosa* - *Larix occidentalis*	Montana	three harvest treatments, and three intensities of slash removal. Only minor effects were seen on streamwater chemistry over 2 post-cutting years. For a 70 yr rotation, the site can sustain production without a significant loss of nutrient capital for a calculated period of 40,000 years.	Stark, 1980b

TABLE 16. Nutrient removals with whole-tree harvested biomass, expressed relative to total inputs, net fluxes, and soil pools. One-year rotation of a hybrid Populus clone.

Category	Biomass	N	P	K	Ca	Mg	Source
HARVEST REMOVALS (kg ha^{-1} 100 yr^{-1})							
whole-tree clear-cut	1,000,000	8600	1300	4400	5800	1600	Hansen and Baker, 1979
INPUTS (kg ha^{-1} 100 yr^{-1})							
a) precipitation		600	40	170	720	170	Chapter 4a, average
b) weathering		0	60	500	1800	500	Chapter 4c, average
c) N_2 fixation		1000	-	-	-	-	Chapter 4d, average
d) total inputs		1600	100	670	2520	670	
NET FLUX (kg ha^{-1} 100 yr^{-1})		700	30	-60	-700	-200	Chapter 5, average
SOIL POOL (kg ha^{-1})							
a) total, rooting zone (53cm)		13,600	3,400	24,300	13,500	9,100	Freedman et al., 1980; good hardwood site
b) available, rooting zone		80	250	140	290	55	
whole-tree harvest, % of total inputs		538%	1300%	657%	230%	239%	
whole-tree harvest, % of net flux		1230	4300	-7300	-829	-800	
whole-tree harvest, % of total soil		63	38	18	43	18	
whole-tree harvest, % of available soil		10800	520	3140	2000	2900	

TABLE 17. Nutrient removals with harvested biomass by intensive harvest techniques, expressed relative to total inputs, net fluxes, and soil pools. Seven-year rotation of Populus deltoides.

Category	Biomass	N	P	K	Ca	Mg	Source
HARVEST REMOVALS (kg $ha^{-1}100\ yr^{-1}$)							
a) conventional clear-cut	-	1343	214	1414	3229	343	White, 1974
b) whole-tree clear-cut	-	2986	414	2529	4971	529	
INPUTS (kg ha^{-1} 100 yr^{-1})							
a) precipitation		600	40	170	720	170	Chapter 4a, average
b) weathering		0	60	500	1800	500	Chapter 4c, average
c) N_2 fixation		1000	-	-	-	-	Chapter 4d, average
d) total inputs		1600	100	670	2520	670	
NET FLUX (kg ha^{-1} 100 yr^{-1})		700	30	-60	-700	-200	Chapter 5, average
SOIL POOL (kg ha^{-1})							
a) total, rooting zone (53 cm)		13,600	3400	24,300	13,500	9100	Freedman et al., 1980;
b) available, rooting zone		86	250	140	290	55	good hardwood site
Conventional removal, % of total inputs		84 %	214 %	211 %	128 %	51 %	
whole-tree removal, % of total inputs		187	414	377	197	79	
conventional removal, % of net flux		192	713	-2357	-461	-172	
whole-tree removal, % of net flux		427	1380	-4215	-710	-265	
conventional removal, % of total soil		10	6	6	24	4	
whole-tree removal, % of total soil		22	12	10	37	6	
conventional removal, % of available soil		1562	86	1010	1110	624	
whole-tree removal, % of available soil		3472	166	1810	1714	962	

TABLE 18. Nutrient removals with harvested biomass by intensive harvest techniques, expressed relative to total inputs, net fluxes, and soil pools. Twenty-nine year rotation of mixed intolerant hardwoods.

Category	Biomass	N	P	K	Ca	Mg	Source
HARVEST REMOVALS (kg ha^{-1} $100yr^{-1}$)							
a) conventional clear-cut	243,000	593	76	324	790	70	Ribe, 1974
b) whole-tree clear-cut	275,000	817	111	441	976	101	
INPUTS (kg ha^{-1} 100 yr^{-1})							
a) precipitation		600	40	170	720	170	Chapter 4a,avg.
b) weathering		0	60	500	1800	500	Chapter 4c, avg.
c) N_2 fixation		1000	-	-	-	-	Chapter 4d, avg.
d) total inputs		1600	100	670	2520	670	
NET FLUX(kg ha^{-1} 100 yr^{-1})		700	30	-60	-700	-200	Chapter 5, avg.
SOIL POOL (kg ha^{-1})							
a) total, rooting zone (50 cm)		8700	3000	19,700	14,900	5250	Freedman et al., 1980. Average hardwood stand
b) available, rooting zone		75	180	120	350	60	
conventional removal, % of total inputs		37%	76%	48%	31%	10%	
whole-tree removal, % of total inputs		51	111	66	39	15	
conventional removal, % of net flux		85	253	-540	-113	-35	
whole-tree removal, % of net flux		117	370	-735	-139	-51	
conventional removal, % of total soil		6.8	2.5	1.6	5.3	1.3	
whole-tree removal, % of total soil		9.4	3.7	2.2	6.6	1.9	
conventional removal, % of available soil		791	42	270	226	117	
whole-tree removal, % of available soil		1089	62	368	279	168	

TABLE 19. Nutrient removals with harvested biomass by intensive harvest techniques, expressed relative to total inputs, net fluxes, and soil pools. Forty-year rotation of a red pine plantation.

Category	Biomass	N	P	K	Ca	Mg	Source
HARVEST REMOVALS (kg ha^{-1} 100 yr^{-1})							
a) conventional clear-cut	400,000	388	38.3	210	463	86	Alban et al., 1978
b) whole-tree clear-cut	498,000	865	105	438	728	145	
c) complete-tree clear-cut	608,000	1053	125	513	838	180	
INPUTS (kg ha^{-1} 100 yr^{-1})							
a) precipitation		600	40	175	720	170	Chapter 4a, average
b) weathering		0	60	500	1800	500	Chapter 4c, average
c) N_2 fixation		1000	-	-	-	-	Chapter 4d, average
d) total inputs		1600	100	670	2520	670	
NET FLUX (kg ha^{-1} 100 yr^{-1})		700	30	-60	-700	-200	Chapter 5, average
SOIL POOL (kg ha^{-1})							
a) total, rooting zone (46 cm)		5800	2000	15,000	8100	2800	Freedman et al., 1980;
b) available, rooting zone		70	140	100	190	40	average softwood stand
conventional removal, % of total inputs		24%	38%	31%	18%	13%	
whole-tree removal, % of total inputs		54	105	65	29	22	
complete-tree removal, % of total inputs		66	125	77	33	27	
conventional removal, % of net flux		55	128	-350	-66	-43	
whole-tree removal, % of net flux		124	350	-730	-104	-73	
complete-tree removal, % of net flux		150	417	-855	-120	-90	
conventional removal, % of total soil		6.7	1.9	1.4	5.7	3.1	
whole-tree removal, % of total soil		15	5.3	3.2	9.0	5.2	
complete-tree removal, % of total soil		18	6.3	3.4	10.3	6.4	
conventional removal, % of available soil		554	27	210	244	214	
whole-tree removal, % of available soil		1330	75	438	383	363	
complete-tree removal, % of available soil		1500	89	513	441	450	

TABLE 20. Nutrient removals with harvested biomass by intensive harvest techniques, expressed relative to total inputs, net fluxes, and soil pools. Fifty-five year rotation of tolerant northern hardwoods.

Category	Biomass	N	P	K	Ca	Mg	Source
HARVEST REMOVALS (kg ha^{-1} 100 yr^{-1})							
a) conventional clear-cut	75,000	244	20	129	351	34	Whittaker et al,1979
b) whole-tree clear-cut	110,000	675	64	282	733	69	
c) complete-tree clear-cut	133,000	1004	160	396	916	93	
INPUTS (kg ha^{-1} 100 yr^{-1})							
a) precipitation		600	40	170	720	170	Chapter 4a, average
b) weathering		0	60	500	1800	500	Chapter 4c, average
c) N_2 fixation		1000	-	-	-	-	Chapter 4d, average
d) total inputs		1600	100	670	2520	670	
NET FLUX (kg ha^{-1} 100 yr^{-1})		700	30	-60	-700	-200	Chapter 5, average
SOIL POOL (kg ha^{-1})							
a) total, rooting zone (50 cm)		8700	3000	19,700	14,900	5250	Freedman et al., 1980;
b) available, rooting zone		75	180	120	350	60	average hardwood stand
conventional removal, % of total inputs		15%	20%	19%	14%	5%	
whole-tree removal, % of total inputs		42	64	42	29	10	
complete-tree removal, % of total inputs		63	160	59	36	14	
conventional removal, % of net flux		35	150	-215	-50	-17	
whole-tree removal, % of net flux		96	213	-470	-105	-35	
complete-tree removal, % of net flux		143	533	-660	-131	-47	
conventional removal, % of total soil		2.8	0.7	0.7	2.4	0.6	
whole-tree removal, % of total soil		7.8	2.1	1.4	4.9	1.3	
complete-tree removal, % of total soil		11.5	5.3	2.0	6.1	1.8	
conventional removal, % of available soil		325	11	108	100	57	
whole-tree removal, % of available soil		900	36	235	209	115	
complete-tree removal, % of available soil		1339	89	330	262	155	

TABLE 21. Nutrient removals with harvested biomass by intensive harvest techniques, expressed relative to total inputs, net fluxes, and soil pools. All-aged stand of red spruce-balsam fir.

Category	Biomass	N	P	K	Ca	Mg	Source
HARVEST REMOVALS (Kg ha^{-1} 100 yr^{-1})							
a) conventional clear-cut	118,000	120	18.2	76	219	20.4	Freedman et al. 1981
b) whole-tree clear-cut	153,000	239	35.2	133	337	36.9	
INPUTS (kg ha^{-1} 100 yr^{-1})							
a) precipitation		600	40	170	720	170	Chapter 4a, average
b) weathering		0	60	500	1800	500	Chapter 4c, average
c) N_2 fixation		1000	-	-	-	-	Chapter 4d, average
d) total inputs		1600	100	670	2520	670	
NET FLUX (kg ha^{-1} 100 yr^{-1})		700	30	-60	-700	-200	Chapter 5, average
SOIL POOL (kg ha^{-1})							
a) total, rooting zone (39 cm)		3760	1280	13,400	5750	1770	Freedman et al. 1981
b) available, rooting zone		47	105	73	110	39	
conventional removal, % of total inputs		8%	18%	11%	9%	3.0%	
whole-tree removal, % of total inputs		15	35	20	13	5.5	
conventional removal, % of net flux		17	61	-127	-31	-10	
whole-tree removal, % of net flux		34	117	-222	-48	-18	
conventional removal, % of total soil		3.2	1.4	0.6	3.8	1.2	
whole-tree removal, % of total soil		6.4	2.8	1.0	5.9	2.1	
conventional removal, % of available soil		255	17	105	199	52	
whole-tree removal, % of available soil		509	34	182	306	95	

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